Beyond average temperature: distribution of wintering birds at multiple scales

Más allá de la temperatura promedio: distribución de aves invernantes a múltiples escalas

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TESIS DOCTORAL
Madrid 2013

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PhD Thesis

Universidad Autónoma de Madrid, September 2013

A efectos bibliográficos la obra debe citarse como sigue:

Villén-Pérez S. 2013 Beyond average temperature: distribution of wintering birds at multiple scales. PhD Thesis.University Autónoma of Madrid, Madrid (Spain)

Villén-Pérez S. 2013. Más allá de la temperatura promedio: distribución de aves invernantes a múltiples escalas. Tesis Doctoral. Universidad Autónoma de Madrid, Madrid (España)

Fotografías cortesía de: Luis M. Carrascal (paisajes) y Javier Lobón (aves)
Maquetación: Sara Villén Pérez

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Memoria presentada por la Licenciada en Biología Sara Villén Pérez
para optar al título de Doctora en Ecología por la Universidad Autónoma de Madrid a través del Programa de Doctorado en Ecología UAM-UCM

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A mis padres

La curiosidad que lleva al hombre a investigar y a viajar son del mismo orden;
responden ambas al imperioso deseo de conocer y comprender el mundo
Luis Carandell

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Contenidos

Thesis abstract

Aim To disentangle the subtleties of the relationship between the thermal environment and the distribution of wintering birds, at multiple spatial scales. Specifically, to analyze the relative influence of temperature on species distributions, its interaction with various thermal and non-thermal factors, and the context-dependence of these relationships (i.e., species, season and geographical location).

Location Iberian Peninsula and Guadarrama Mountain range (central Spain).

Methods I use observational and experimental field approaches to control for habitat structure, topography, food abundance and predation risk, from forest patches to landscape, regional and peninsular scales. Fieldwork is carried out with woodland passerines inhabiting mountain oakwoods of *Quercus pyrenaica*, and subtle variations in temperature and wind are precisely measured with data loggers.

Main results and conclusions Wintering birds respond to natural variations in temperature at multiple scales, selecting the warmest forest patches to forage and the warmest mountain areas and peninsular regions to overwinter. However, temperature *per se* accounts for a relatively small proportion of the variation in species distribution patterns. Indeed, a sudden extreme drop in temperature is not enough to alter species abundances, or to promote their redistribution to minimize wind chill. Other non-thermal environmental factors like vegetation structure, predation risk and availability of predictable food resources, seem to be more deterministic in driving winter species distribution than direct measurements of temperature. On the other hand, the influence of the thermal environment goes far beyond average temperature: minimum night temperature, incident sun radiation and altitude related with snow cover are key drivers of species distributions. The relative relevance of all these factors depends on the ecological scenario, varying across species, seasons and geographical locations. I conclude that if we disregard other environmental effects, we will overestimate the influence of temperature on species abundance and underestimate the plasticity of these to respond to temperature changes.

Applications and prospects Fine-grained approaches, based on direct measures of the study organisms and carried out through precise local measurements of environmental variables, are needed to understand the functional mechanisms driving species distribution patterns at wider scales. At all scales, we need to control for other environmental factors when predicting the responses of birds to temperature, under either current or future scenarios of global warming. Otherwise, we are at risk of generating strongly biased predictions that will inflate the magnitude of climate change effects.

Resumen de la tesis

Objetivo *Desentrañar los pormenores de la relación entre el ambiente térmico y la distribución de aves invernantes a múltiples escalas espaciales. En concreto, analizar la influencia relativa de la temperatura en la distribución de especies, su interacción con varios factores térmicos y no térmicos, y cómo tales relaciones dependen del contexto ecológico (i.e., especies involucradas, estación del año y localización geográfica).*

Localización *Península Ibérica y Sierra de Guadarrama (centro de España).*

Métodos *He utilizado tanto aproximaciones observacionales como experimentales de campo para controlar el efecto de la estructura del hábitat, la topografía, la abundancia de alimento y el riesgo de depredación, en escalas que varían desde el parche hasta el paisaje forestal, la región de Guadarrama y la Península Ibérica. El trabajo de campo se ha llevado a cabo con paseriformes forestales de robledales montanos de Quercus pyrenaica, y las variaciones de temperatura y viento se han medido de forma precisa y local con registradores de datos.*

Resultados y conclusiones principales *Las aves invernantes responden a variaciones naturales en la temperatura a múltiples escalas, seleccionando los parches forestales más cálidos para forrajear y las áreas de la sierra y de la península más cálidas para pasar el invierno. Sin embargo, la temperatura "per se" explica una proporción relativamente pequeña de la variación en los patrones de distribución de especies. De hecho, una caída extrema y repentina de la temperatura no es suficiente para alterar la abundancia de las especies, ni para promover su redistribución hacia las áreas con una sensación térmica más alta. Otros factores ambientales como la estructura de la vegetación, el riesgo de depredación y la disponibilidad de fuentes predecibles de alimento, son más deterministas en la distribución invernal de especies que las medidas directas de temperatura. Por otro lado, la influencia del ambiente térmico va más allá de la temperatura promedio: la temperatura mínima nocturna, la radiación solar incidente y la altitud relacionada con la cobertura de nieve son determinantes clave en la distribución de las especies. La importancia relativa de todos estos factores depende del escenario ecológico, variando a través de las especies, las estaciones del año y de las localizaciones geográficas. Mi conclusión es que si no consideramos otros efectos ambientales, estaremos sobreestimando la influencia de la temperatura en la abundancia de especies y subestimando la plasticidad de estas para responder a cambios de temperatura.*

Aplicaciones y perspectivas *Las aproximaciones de detalle, basadas en medidas directas de los organismos de estudio y en medidas locales precisas de las variables ambientales, son necesarias para entender los mecanismos funcionales que dirigen los patrones de distribución de especies a escalas mayores. A cualquier escala, necesitamos controlar la influencia de otros factores ambientales sobre la respuesta de las aves a la temperatura, bajo escenarios tanto actuales como de cambio global futuros. En caso contrario, corremos el riesgo de generar predicciones fuertemente sesgadas que inflen la magnitud de los efectos del cambio climático.*

List of original publications

Lista de publicaciones originales

This PhD thesis is based on seven original research articles in which I have significantly contributed, with increasing prominence, in conceiving the idea, designing the study, collecting and analyzing data, discussing results and writing the manuscripts. Five of them are already published in international forums by the date of this thesis dissertation.

Esta tesis se basa en siete artículos originales de investigación a los que he contribuido de forma significativa, y cada vez con mayor protagonismo, concibiendo la idea, diseñando el estudio, tomando y analizando los datos, discutiendo los resultados y escribiendo los manuscritos. Cinco de ellos están publicados en foros internacionales a fecha de la disertación de esta tesis.

Chapter 1. Villén-Pérez S, Carrascal LM, Seoane J (2013) Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit. *PlosOne* 8(7): e68448

Chapter 2. Villén-Pérez S, Carrascal LM, Gordo O (2013) Wintering forest birds roost in areas of higher sun radiation. *European Journal of Wildlife Research* doi:10.1007/s10344-013-0750-7

Chapter 3. Villén-Pérez S, Carrascal LM. Woodland Mediterranean birds can resist an extreme cold wave *(Manuscript)*

Chapter 4. Carrascal LM, Villén-Pérez S, Seoane J (2012) Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. *Ecological Research* 27: 293-302

Chapter 5. Carrascal LM, Seoane J, Villén-Pérez S (2012) Temperature and food constraints in wintering birds - an experimental approach in montane Mediterranean oakwoods. *Community Ecology* 13: 221-229

Chapter 6. Seoane J, Villén-Pérez S, Carrascal LM (2013) Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods. *Ecological Research* 28: 435-445

Chapter 7. Villén-Pérez S, Carrascal LM, Palomino D. Bioclimatic models can provide misleading projections when derived only from climatic predictors *(Manuscript)*

Prologue

A competences-acquisition process

The development of this PhD thesis is contemplated as a holist and open learning process, where the most important idea is not the final product but the journey and the baggage of competences acquired throughout the process. As usual in the generation of scientific knowledge, here I contribute with some new ideas and provide evidence to support others already existing in the body of knowledge of a specific scientific area. Therefore, the text you are reading now will probably have relatively modest scope and impact on the scientific community. The technical super-specialized knowledge that can be developed in a pre-doctoral period may be of little utility beyond this period in a field as wide as Ecology, and there will probably be the acquired skills that will be the base of a future scientific career. For these reasons the final objective of my pre-doctoral period has not exclusively been the fulfillment of a series of scientific studies and their materialization in scientific publications on international forums, but the training and the acquisition of the relevant skills to develop a scientific career as an independent researcher.

First, I have worked on my critical thinking of knowledge and how it is generated. I have pursued this by reading scientific literature, by the reiterated questioning the own and others' work, and by participating in the publication process as both an author and a reviewer of others' work, and by the exercise of scientific discussion in formal and informal forums. Second, by an increased assumption of responsibilities throughout the research works developed along this period, I have learned to conceive, design and develop a complete and original research project in the field of Ecology. This means initiative and independence to generate ideas and to develop them, to extract conclusions and to communicate them, and to confront both intellectual and logistic problems. And this within a small research group, in which each project requires big doses of individual initiative, courage and collaboration to go on.

This academic training has been developed following the thesis statement exposed below as a guide. To enrich the process, I have use multiple approaches to the theme, analyzing the study hypothesis in relation to diverse biological processes, at different spatial and temporal scales, using both observational and experimental approaches, and a wide variety of techniques for sampling and data analysis. Moreover, I have enjoyed the opportunities afforded by the *Subprograma de Estancias Breves FPI* to interact with foreign research groups, learning from others' manners of working and discovering other peripheral disciplines. As a whole, it has been a process of recognizing virtues and strengthening lacks; a process of learning to understand what is already known and to explore what is still unknown. In conclusion, this Doctorate in Ecology has been outlined as a period of specific but diverse training, which is not exclusively focused on the generation of knowledge in a specific topic but in the preparation for a future research career.

Prólogo

Un proceso de adquisición de competencias

El desarrollo de esta Tesis Doctoral se plantea como un proceso holista y abierto de aprendizaje, donde lo más importante no es el producto final sino el recorrido y el bagaje de competencias adquiridas a lo largo del proceso. Como es habitual en la generación de conocimiento científico, aquí se aportan algunas ideas nuevas y se ofrece evidencia para consolidar otras ya existentes en el cuerpo de conocimiento de un área científica concreta. Por tanto, es probable que el texto que tiene usted entre manos tenga un alcance y un impacto en la comunidad científica relativamente modestos. Por otra parte, es posible que el conocimiento técnico super-especializado que se puede llegar a desarrollar en una fase pre-doctoral no resulte de gran utilidad más allá de este periodo en un campo tan amplio como el de la Ecología, y probablemente serán las destrezas adquiridas las que cimenten el futuro de una carrera científica. Por estas razones, el objetivo último de mi periodo pre-doctoral no ha sido exclusivamente la realización de una serie de estudios científicos y su materialización en publicaciones científicas en foros internacionales, sino la capacitación y la adquisición de las destrezas necesarias para desarrollar una carrera científica como investigadora independiente.

En primer lugar, he trabajado en el desarrollo de mi pensamiento crítico hacia el conocimiento y hacia cómo éste se genera. Esto lo he perseguido a través de la lectura de la literatura científica, del cuestionamiento reiterado del trabajo propio y ajeno, de la participación en el proceso de publicación como autora y como revisora del trabajo de otros, y del ejercicio de discusión científica en foros más o menos formales. En segundo lugar, a través de una creciente toma de responsabilidades a lo largo de los trabajos de investigación desarrollados durante este periodo, he aprendido a concebir, diseñar y desarrollar un proyecto de investigación original completo en el campo de la Ecología. Esto supone iniciativa e independencia para generar ideas y desarrollarlas, para extraer conclusiones y comunicarlas, y para enfrentarse a los problemas tanto intelectuales como logísticos. Y todo ello en el seno de un grupo de investigación pequeño, en el que cada proyecto requiere grandes dosis de colaboración, iniciativa y coraje individuales para salir adelante.

Esta formación se ha desarrollado siguiendo como hilo conductor el enunciado de la tesis que se expondrá en la introducción. Para enriquecer el proceso se han buscado múltiples enfoques del tema, analizando las hipótesis de estudio en relación con diversos procesos biológicos, a distintas escalas tanto espaciales como temporales, utilizando aproximaciones tanto observacionales como experimentales, y una amplia variedad de técnicas de muestreo y de análisis de datos. Además he aprovechado las oportunidades que me ha brindado el Subprograma de Estancias Breves FPI para interactuar con grupos de investigación extranjeros, enriqueciéndome con el descubrimiento de otras formas de trabajar y de otras disciplinas periféricas a la Ecología. En conjunto ha sido un proceso de reconocimiento de virtudes y fortalecimiento de carencias, de aprender a entender lo que ya se conoce y de aprender a explorar lo que aún no se conoce. En conclusión, este Doctorado en Ecología se ha planteado como un periodo de formación específica pero diversa, que no se centra exclusivamente en la ampliación del conocimiento sobre una materia, sino en la capacitación para una futura carrera investigadora.

Introduction

Introducción

Introduction

Theoretical background

Species distributions in temperate ecosystems are strongly influenced by environmental temperature at various scales (e.g., Shields and Grubb 1974, Root 1988, Wachob 1996, Meehan et al. 2004, Evans et al. 2006, Butler et al. 2007, Davies et al. 2007, Kalmar and Currie 2007, Whittaker et al. 2007, Moreno-Rueda and Pizzarro 2008, Quian et al. 2010, Velky et al. 2010, Zuckerberg et al. 2011). This may be especially true in the energy-limiting period of winter, in which food resources are scarce, the time available for foraging is shortened, adverse weather conditions are unpredictable, and the low temperatures continuously challenge homeothermic animals (Gibb 1954, Fretwell 1972, Calder and King 1974; Figure 1; Figure 2). Survival in this scenario depends on maintaining a positive energy balance, obtaining enough food for self-maintenance and reducing the metabolic costs of thermoregulation (e.g. Newton 1998, Rogers and Reed 2003, Cuthill and Houston 2008). Thus, species are expected to overwinter at warmer areas, where thermoregulation costs are reduced and the foraging environment is indirectly improved (i.e., higher fruit production, higher arthropod activation and reduced snow cover on foraging substrates; Honek et al. 1997, Avery and Krebs 1984, Carrascal et al. 2001, Robinson et al. 2007).

The current determination of ecologists to forecast global warming effects on species distribution ranges and abundances puts the emphasis on the effect of temperature (e.g., Peterson et al. 2002, Thomas et al. 2004; see Huntley et al. 2007 and Araújo et al. 2012 for the distribution of breeding birds in Europe and in the Iberian Peninsula, respectively), because the large availability of data and models makes it the environmental factor that is most easily projected under future scenarios of climate change. However, animal distributions are also driven by other factors related to food availability, predation risk, the biogeographical history or the habitat preferences of species (e.g., Hilton et al. 1999, Carrascal et al. 2001, Rahbeck and Graves 2001, Canterbury 2002, Heikkinen et al. 2004, Seoane et al. 2004, Rahbeck et al. 2007, Robinson et al. 2007, Carnicer and Díaz-Delgado 2008, Cresswell et al. 2009, Honkanen et al. 2010, Aragon et al. 2010 , Carrascal and Palomino 2012), for which there is a lack of well calibrated models to predict future

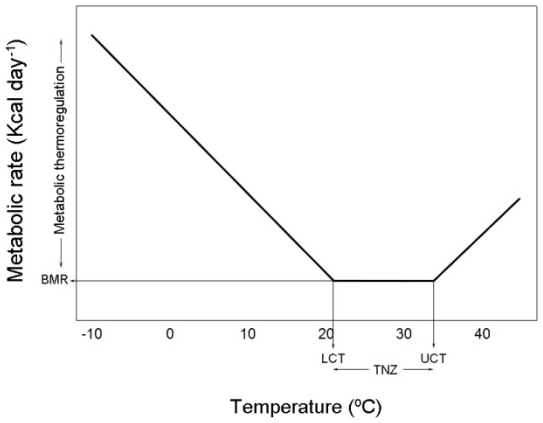

Figure 1. Below the lower critical temperature (LCT), the metabolic costs of thermoregulation linearly increase at decreasing air temperatures. UCT: Upper critical temperature; TNZ: thermoneutral zone; BMR: basal metabolic rate. Represented values of LCT and UCT are approximates for the studied species of forest passerines (Kendeigh et al. 1977).

Figura 1. Por debajo de la temperatura crítica mínima (LCT), los costes metabólicos de termorregulación aumentan de forma lineal al descender la temperatura del aire. *Eje de ordenadas: tasa metabólica (Kcal día^{-1}); eje de abcisas: temperatura (ºC). UCT: temperatura crítica máxima; TNZ: zona de termoneutralidad; BMR: tasa metabólica basal; Metabolic thermoregulation: termorregulación metabólica. La gráfica representa valores aproximados de LCT y UCT para los paseriformes forestales de estudio (Kendeigh et al. 1977).*

changes (Busch 2006, Rounsevell et al. 2006, Spangenberg et al. 2012). Moreover, there are other factors related to the thermal environment experienced by an organism ('thermal factors' hereafter), such as wind and sun radiation, that strongly influence the metabolism and behavior of species (Lustick et al. 1970, 1978, De Jong 1976, Ohmart and Lasiewsk 1971, Wood and Lustick 1989, Bakken 1990, Wolf and Walsberg 1996, Dolby and Grubb 1999, Wolf et al. 2000, Kilpatrick 2003), but that are rarely considered in species distributions models (see some exceptions in Shields and Grubb 1974, Stapanian et al. 1999, Carrascal et al. 2001, Huertas and Díaz 2001, Carrascal and Díaz 2006, Carrascal and Seoane 2009, Quan et al. 2011).

The role of these environmental factors has been mostly examined at coarse-grained scales, considering cells of hundreds or thousands of square km that comprise heterogeneous environments and microclimates (Suggitt et al. 2011), and using temperature data interpolated from a few meteorological stations. In these studies, climate seems to constrain distributions at broader scales (e.g., 50×50 Km), while habitat-related factors dominate at finer scales (e.g., 10 Km; Whittaker et al. 2001, Willis and Whittaker 2002, Luoto et al. 2007). Evidence gets scarcer at even smaller scales, and it is not clear whether the effect of temperature progressively disappear at finer resolutions.

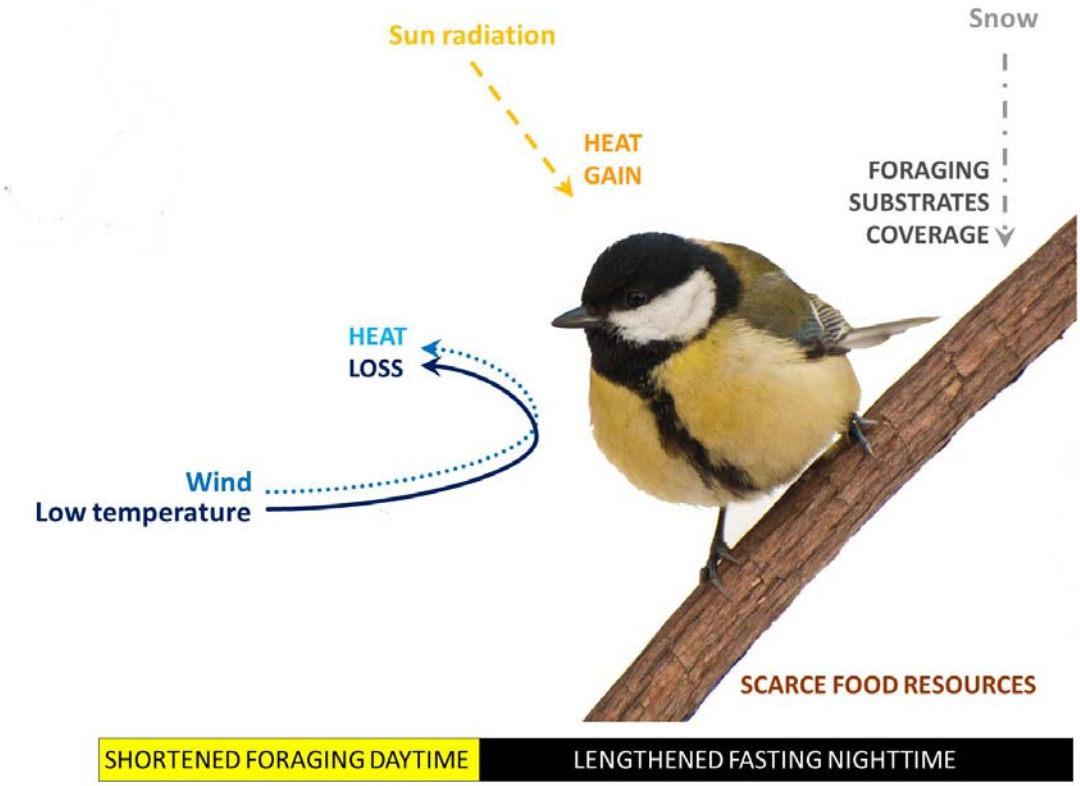

Figure 1. The winter environment of a small endotherm. The length of yellow and black bars is related to the duration of day and nighttime, respectively, in the study area during the winter solstice. *Picture of Great tit courtesy of J. Lobón.*

Figura 1. El panorama invernal de un pequeño endotermo. *La longitud de las barras amarilla y negra se relaciona con la duración del día y la noche, respectivamente, en el área de estudio durante el solsticio de invierno. Low temperature: baja temperatura; Wind: viento; Sun radiation: radiación solar; Snow: nieve; Heat loss: pérdida de calor; Heat gain: ganancia de calor; Foraging substrates coverage: cobertura de los sustratos de forrajeo; Scarce food resources: Escasez de fuentes de alimento; Shortened foraging daytime: acortamiento del tiempo diurno de forrajeo; Lengthened fasting nighttime: alargamiento del tiempo nocturno de ayuno. Fotografía de Carbonero común cortesía de J. Lobón.*

Thesis statement

The influence of temperature on species distributions is at risk of becoming a dogma that oversimplifies the underlying ecological processes and underestimates the relevance of other environmental factors. Species may respond in a multifactorial way to their thermal environments, including temperature but also sun radiation, wind and altitude related to snow cover. Indeed, this response might be mediated by other environmental factors related with predation risk, food resources or habitat preferences of species, and these factors might be even more important than the thermal environment *per se* in some circumstances. The relative importance of every side of this multifactorial picture might depend on the characteristics of the ecological scenario, including the spatial scale, the biological processes involved, the natural history of species, the phase of their life cycles and the course of extreme climatic events

Thesis Outline

This thesis aims at disentangling the subtleties of the relationship between the thermal environment and the distribution of birds wintering in the Iberian Peninsula, with a special emphasis on small woodland birds of Guadarrama mountains (see Box 1). The objective is to analyze the relevance of various thermal attributes, their interaction with other environmental factors and the context-dependence of these relationships (Table 1).

First, I wonder whether temperature is as relevant as generally stated in determining the distribution of species, and what is the magnitude of its importance in relation to other thermal and non-thermal factors. This question provides the backbone of this thesis. The relevance of temperature in defining species distribution is contrasted with the effects of sun radiation [Ch. 2, 6], wind speed [Ch. 3], altitude as a surrogate of harsh weather conditions and snow-cover probability [Ch. 2, 4, 5, 6, 7], habitat structure [Ch. 3, 4, 5, 6, 7], predation risk [Ch. 1] and food availability [Ch. 4, 5]. The purpose is to elucidate how necessary it is to control for other environmental variables when understanding species distributions, under either current or future climate scenarios.

Second, I wonder whether species respond differentially to temperature when varying the spatial scale, and if these responses are analogous in direction and magnitude considering that thermal heterogeneity can vary with scale. The answer to this question will arise from the comparison of the seven chapters of this thesis, which analyze distribution patterns among forest patches [Ch. 1], locations in a forest landscape [Ch. 2, 3], woodlands at a regional scale [Ch. 4, 5, 6] and peninsular areas [Ch. 7] (Table 1, Figure 3). In all chapters up to regional scale [Ch. 1-6], the emphasis is put on detecting responses to subtle spatial variations in temperature precisely measured *in situ* with data loggers.

Third, I wonder whether species will respond differently to day and nighttime temperatures, which might be tightly related to diurnal and nocturnal thermoregulatory costs, respectively, and probably have a more functional meaning than average temperature. To answer this I compare the relative influence of day and nighttime temperatures under different ecological scenarios [Ch. 2, 4, 6]. This will examine whether averages are adequate measurements of the thermal environment, or more specific and meaningful predictors are needed to understand species distributions.

Fourth, I explore whether birds respond to environmental predictors that

Table 1. Synthesis of the approaches used in each chapter of this thesis. Temp.: temperature; Alt.: altitude; Sun: sun radiation; Wind: wind speed; Orient.: cardinal orientation; Veg. structure: vegetation structure: Weather cond.: weather conditions. * The geographical extent (i.e., distance between sampling units under comparison, Whittaker et al. 2001) is referred as 'spatial scale' in the text, as I consider that this is a more intuitive term. Moreover, I have decided not to follow the recommendations of Pearson and Dawson (2003) to indicate the different spatial scales of study, and I have preferred to utilize the terminology presented in this table considering that this is more widely used.

Chapter	Geographical extent (ca. Km) *	Biological scale	Ecological decision	Thermal predictors	Non-thermal predictors	Temporal comparison
1	Local (0.3)	Individual	Foraging patch selection	Temp.	Predation risk	
2	Landscape (1.5)	Guild	Roosting site selection	Temp., Alt., Sun	Veg. structure, Previous residence	
3			Spatial distribution	Temp., Wind	Veg. structure	Weather cond.
4	Regional (50)			Temp., Alt.	Veg. structure, Food abundance	Inter-annual
5				Temp., Alt.	Veg. structure, Food abundance (experimental)	
6		Community		Temp., Alt., Orient.	Veg. structure and leaf phenology	Seasonal
7	Peninsular (1000)	Macroecological		Temp.	Precipitation, Land cover, Topography, Space	

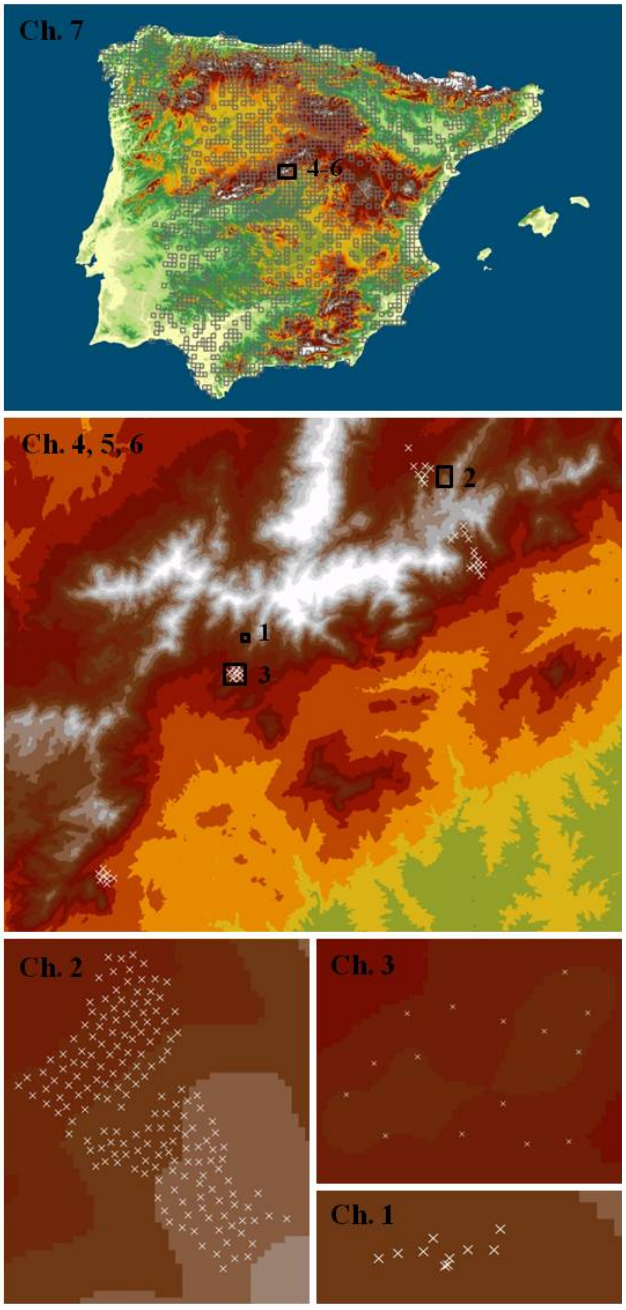

Figure 3. Study areas of this thesis, corresponding to chapters (Ch.) developed from local [Ch. 1] to landscape [Ch. 2, 3], regional [Ch. 4, 5, 6] and peninsular [Ch. 7] scales. For Ch. 7 UTM sampling cells are shown in grey, while for Ch. 1 to 6, sampling points are shown by white crosses. Black squares and adjacent numbers show the location of study areas at finer scales.

***Figura 3. Áreas de estudio de esta tesis**, correspondientes a los capítulos (Ch.) desarrollados a escalas locales [Ch. 1], de paisaje [Ch. 2, 3], regionales [Ch. 4, 5, 6] y peninsulares [Ch. 7]. En Ch. 7 las celdas de muestreo se representan en gris, mientras que en Ch. 1-6 los puntos de muestreo se muestran con cruces blancas. Los cuadrados negros y los números adyacentes señalan la localización de las áreas de estudio a escalas más finas.*

do not imply instantaneous, but rather time lag benefits. Specifically, I analyze the influence of nocturnal temperature on daytime distribution [Ch. 4, 5, 6], the effect of sun radiation and diurnal temperature on roost site selection at nighttime [Ch. 3], and the importance of altitude as a surrogate of harsh weather conditions and snowfall probability [Ch. 2, 4, 5, 6]. These effects would talk about the foresight capability of birds to anticipate winter adversities, thus improving survival probabilities.

Finally, I attempt to understand how the relative importance of each environmental factor driving species distribution varies with the ecological scenario in which it is considered, according to its context-dependent functional meaning. I approach this goal by comparing the relationship between the thermal environment and species distribution on two specific foraging guilds (ground-foraging birds [Ch. 4] vs. tree-gleaning birds [Ch. 5]), at different stages of the annual cycle (winter vs. breeding seasons [Ch. 6]), and under different weather conditions (mild weather vs. cold wave [Ch. 3] and cold vs. warmer winters [Ch. 4]). Moreover, I focus on various ecological decisions (*where to forage* [Ch. 1, 5], *where to roost* [Ch. 2], and *where to reside* [Ch. 3, 4, 5, 6, 7]) analyzed on different biological scales (from individual decisions [Ch. 1], to guild abundance [Ch. 2, 3, 5,], guild and community species richness [Ch. 4, 6], community nestedness [Ch. 6] and macroecological patterns [Ch. 7]). This diverse analytical effort is conceived to untangle whether the generally-assumed role of the thermal environment on winter species distribution can be generalized throughout different ecological scenarios.

Box 1

Why birds?

- Birds are small endotherms prone to rapid heat loss, whose metabolic thermoregulation costs are known to directly increase with decreasing temperatures (Figure 1), increasing wind speed and diminishing sun radiation (see references in the text).
- They adopt a vagabonding lifestyle in winter exploring large areas, and thus have the potential to select the best ones.
- There is a well developed knowledge of their biology, physiology and ecology to support an organism approach (Meehan et al. 2004).
- Birds are easily detectable and abundant enough to obtain good sample sizes with reasonable sampling efforts.

Why the Iberian Peninsula?

- The Iberian Peninsula is an important winter quarter for a great number of bird species from the western Palearctic region (Moreau 1972, Perrins 1998). For this reason, it may be especially interesting to analyze the quality of the winter environment they encounter here.
- Winter ecology of birds has been mainly developed at higher latitudes, where processes may differ from those occurring in the Mediterranean. Here, birds are expected to be less limited in terms of temperature, weather harshness and food availability (Lack 1954, Fretwell 1972, Newton 1998).

Why montane oakwoods?

- Montane areas offer steep gradients in environmental conditions within short distances, due to the adiabatic relation of temperature with altitude, the higher probability of inclement weather and snow-cover at higher altitudes, and the topography influence over wind and sun incidence. Moreover, mountains pose more stringent winter conditions to animals than lowlands.
- Working within homogeneous ecosystems in terms of habitat type (i.e., forests) minimizes the variation in responses due to habitat-type and allows abiotic determinants to stand out.
- Oakwoods (*Quercus pyrenaica*) in the Guadarrama mountain range have been traditionally managed for charcoal and cattle grazing, and this has resulted in a large variety of forests in terms of structure and tree maturity (Costa et al. 1998). Therefore, here it is possible to test the role of vegetation structure on species distributions within a monospecific forest.

Chapters' introduction and PhD candidate-contribution

This thesis is based on seven original research articles, five of which are already published in international forums (see 'List of original publications' in page 13). Although each work is the result of a tight cooperation among co-authors, here I only indicate my contributions.

In Chapter 1 we experimentally quantify the relative importance of thermoregulation and predation risk in foraging patch selection of wintering woodland birds at local scale. I have contributed to this work in conceiving, designing, and performing the experiment, analyzing the data, discussing the results and writing the manuscript.

In Chapter 2 we experimentally analyze the determinants of winter roost site selection by tree-gleaning passerines at landscape scale. I have contributed to this work in conceiving, designing, and performing the experiment, analyzing the data, discussing the results and writing the manuscript.

In Chapter 3 we analyze how an extreme cold wave affected the relative abundance of wintering tree-gleaning birds and their re-distribution at landscape scale. I have contributed to this work in conceiving and designing the study, collecting and analyzing the data, discussing the results and writing the manuscript.

In Chapter 4 we analyze the relative influence of the thermal environment, food availability and habitat structure in winter species richness of ground-foraging woodland birds at regional scale. I have contributed to this work in conceiving and designing the study, collecting and analyzing the data, discussing the results and writing the manuscript.

In Chapter 5 we experimentally disentangle the effects of temperature, food and habitat structure in the winter abundance of tree-gleaning woodland birds at regional scale. I have contributed to this work in conceiving, designing, and performing the experiment, analyzing the data, discussing the results and writing the manuscript.

In Chapter 6 we analyze the influence of biotic and abiotic factors determining species richness and nestedness of oakwood bird communities at regional scale, and compare the magnitude of these effects in winter and spring. I have contributed to this work in conceiving and designing the study, collecting and analyzing the data, discussing the results and writing the manuscript.

In Chapter 7 we analyze the influence of temperature in the abundance of terrestrial birds wintering in the Iberian Peninsula and compare the performance of bioclimatic models that only account for climate vs. those that also account for the environmental preferences of species. I have contributed to this work in conceiving the idea, analyzing the data, discussing the results and writing the manuscript.

In addition to the English original manuscripts, a summary in Spanish can be found at the beginning of each chapter.

Introducción

Antecedentes y estado actual del tema

Las distribuciones de especies en ecosistemas templados están fuertemente influenciadas por la temperatura ambiente a varias escalas (e.g., Shields y Grubb 1974, Root 1988, Wachob 1996, Meehan et al. 2004, Evans et al. 2006, Butler et al. 2007, Davies et al. 2007, Kalmar y Currie 2007, Whittaker et al. 2007, Moreno-Rueda y Pizzarro 2008, Quian et al. 2010, Velky et al. 2010, Zuckerberg et al. 2011). Esto debe cumplirse especialmente durante el invierno, un periodo energéticamente limitante en el que las fuentes de alimento son escasas, el tiempo de forrajeo se acorta, las condiciones climatológicas adversas son impredecibles, y las bajas temperaturas suponen un reto constante para los animales homeotermos (Gibb 1954, Fretwell 1972, Calder y King 1974; Figura 1; Figura 2). En este escenario, la supervivencia depende de un balance energético positivo, que se consigue reduciendo los costes metabólicos de termorregulación y obteniendo suficiente alimento para cubrir las necesidades (e.g., Newton 1998, Rogers y Reed 2003, Cuthill y Houston 2008). Como consecuencia, esperamos que las especies invernen en las áreas más cálidas, donde se reducen los costes de termorregulación y el ambiente de forrajeo es de mejor calidad (i.e., mayor producción de frutos, mayor activación de artrópodos y menor cobertura de nieve en los sustratos de forrajeo; Honek et al. 1997, Avery y Krebs 1984, Carrascal et al. 2001, Robinson et al. 2007).

La preocupación actual de los ecólogos de pronosticar las consecuencias del cambio climático sobre los rangos de distribución y las abundancias de las especies se centra en el efecto de la temperatura (e.g., Peterson et al. 2002, Thomas et al. 2004; ver Huntley et al. 2007 and Araújo et al. 2012 para la distribución de aves reproductoras en Europa y la Península Ibérica, respectivamente), ya que existen gran cantidad de datos y modelos que hacen que ésta sea la variable ambiental más fácil de proyectar bajo escenarios futuros de cambio climático. Sin embargo, las distribuciones animales también dependen de otros factores relacionados con la disponibilidad de alimento, el riesgo de depredación, la historia biogeográfica o las preferencias de hábitat de las especies (e.g., Hilton et al. 1999, Carrascal et al. 2001, Rahbeck y Graves 2001, Canterbury 2002, Heikkinen et al. 2004, Seoane et al. 2004, Rahbeck et al. 2007, Robinson et al. 2007, Carnicer y Díaz-Delgado 2008, Cresswell et al. 2009, Honkanen et al. 2010, Aragon et al. 2010, Carrascal y Palomino 2012), para los cuales no existen modelos bien calibrados que predigan su evolución en el futuro (Busch 2006, Rounsevell et al. 2006, Spangenberg et al. 2012). Además, existen otros factores relacionados con el ambiente térmico que experimenta un organismo (que en lo sucesivo denominaré como 'factores térmicos'), como el viento o la radiación solar, que influyen de forma importante sobre el metabolismo y el comportamiento de las especies (Lustick et al. 1970, 1978, De Jong 1976, Ohmart y Lasiewsk 1971, Wood y Lustick 1989, Bakken 1990, Wolf y Walsberg 1996, Dolby y Grubb 1999, Wolf et al. 2000, Kilpatrick 2003), pero que raramente se consideran en los modelos de distribución de especies (ver algunas excepciones en Shields y Grubb 1974, Stapanian et al. 1999, Carrascal et al. 2001, Huertas y Díaz 2001, Carrascal y Díaz 2006, Carrascal y Seoane 2009, Quan et al. 2011).

Tabla 1. Síntesis de las aproximaciones utilizadas en cada capítulo de esta tesis. *Temp.: temperatura; Alt: altitud; Sol: radiación solar; Viento: velocidad del viento; Orient: orientación cardinal; Estructura veg.: estructura de la vegetación. * En el texto utilizo 'escala espacial' para referirme a la extensión geográfica (i.e., distancia entre unidades muestrales comparadas, Whittaker et al. 2001), ya que considero que este es un término más intuitivo. De la misma forma, he decidido no seguir las recomendaciones de Pearson y Dawson (2003) para referirme a las distintas escalas espaciales de estudio, y he preferido utilizar la terminología que se presenta en esta tabla considerando que este es su uso más generalizado.*

Capítulo	***Extensión geográfica (ca. Km)****	***Escala biológica***	***Decisión ecológica***	***Predictores térmicos***	***Predictores no térmicos***	***Comparación temporal***
1	*Local (0.3)*	*Individual*	*Selección parche forrajeo*	*Temp.*	*Riesgo de depredación*	
2	*Paisaje (1.5)*	*Gremio*	*Selección dormidero*	*Temp., Alt., Sol*	*Estructura veg., Residencia previa*	
3			*Distribución espacial*	*Temp., Viento*	*Estructura veg.*	*Condiciones climáticas*
4	*Regional (50)*			*Temp., Alt.*	*Estructura veg., Abundancia de alimento*	*Inter-anual*
5				*Temp., Alt.*	*Estructura veg., Abundancia de alimento (experimental)*	
6		*Comunidad*		*Temp., Alt., Orient.*	*Estructura veg., Fenología de foliación*	*Estacional*
7	*Peninsular (1000)*	*Macroecológica*		*Temp.*	*Precipitación, Uso del suelo, Topografía, Espacio*	

El papel de estos factores ambientales se ha examinado principalmente a escalas amplias (de "grano grueso"), considerando celdas de cientos o miles de km cuadrados que comprenden una gran variedad de ambientes y microclimas (Suggitt et al. 2011), y utilizando datos de temperatura interpolados a partir de unas cuantas estaciones meteorológicas. En estos estudios, el clima parece ser el limitante a gran escala (e.g., 50×50 Km), mientras que los factores relacionados con el hábitat dominan a las escalas más finas (e.g., 10 Km; Whittaker et al. 2001, Willis y Whittaker 2002, Luoto et al. 2007). Las evidencias disminuyen al afinar la resolución, y no queda claro si el efecto de la temperatura desaparece progresivamente en las escalas más bajas.

Enunciado de la tesis

La influencia de la temperatura en la distribución de especies corre el riesgo de convertirse en un dogma que sobre-simplifique los procesos ecológicos subyacentes y subestime la relevancia de otros factores ambientales. Las especies deben responder a sus ambientes térmicos de una manera multifactorial, incluyendo la temperatura pero también la radiación solar, el viento y la altitud relacionada con la cobertura de nieve. De hecho, esta respuesta debe estar mediada por otros factores ambientales relacionados con el riesgo de depredación, las fuentes de alimento o las preferencias de hábitat de las especies, llegando a ser incluso más importantes que el ambiente térmico "per se" en algunas circunstancias. La importancia relativa de cada cara de este panorama multifactorial debe depender de las características del escenario ecológico, incluyendo la escala espacial, los procesos biológicos involucrados, la historia natural de las especies, la fase de sus ciclos de vida y la ocurrencia de eventos climatológicos extremos.

Presentación de la tesis

Esta tesis pretende desentrañar los pormenores de la relación entre el ambiente térmico y la distribución de las aves invernantes en la Península Ibérica (ver Cuadro 1), prestando una atención especial a las aves forestales de la Sierra de Guadarrama. El objetivo es analizar la relevancia de varios atributos térmicos, su interacción con otros factores ambientales y como estas relaciones dependen del contexto en el que se consideren (Tabla 1).

En primer lugar me pregunto si la temperatura es tan relevante determinando la distribución de especies como se suele asumir, y cuál es la magnitud de su importancia en relación con otros factores ambientales tanto térmicos como no térmicos. Esta pregunta constituye la espina dorsal de esta tesis. La relevancia de la temperatura definiendo la distribución de especies se contrasta con los efectos de la radiación solar [Cap. 2, 6], la velocidad del viento [Cap. 3], la altitud como variable subrogada de las condiciones climatológicas adversas y de la cobertura de nieve [Cap. 2, 4, 5, 6, 7], la estructura del hábitat [Cap. 3, 4, 5, 6, 7], el riesgo de depredación [Cap. 1] y la disponibilidad de alimento [Cap. 4, 5]. El propósito es elucidar hasta qué punto es necesario controlar la influencia de otras variables ambientales al entender las distribuciones de especies, bajo escenarios climáticos tanto actuales como futuros.

En segundo lugar me planteo si las especies responden de forma diferente a la temperatura al variar la escala espacial, y si estas respuestas son análogas en dirección y magnitud considerando que la heterogeneidad térmica puede variar con la escala. La respuesta a esta pregunta emergerá de la comparación de los siete capítulos de la tesis, en los que se analizan patrones de distribución entre

parches forestales [Cap. 1], zonas de un

Cuadro 1.

¿Por qué aves?

- *Las aves son pequeños endotermos susceptibles de pérdidas de calor rápidas, cuyos costes metabólicos aumentan directamente al descender las temperaturas (Figura 1), aumentar la velocidad del viento y disminuir la radiación solar (ver referencias en el texto).*
- *En invierno adoptan un estilo de vida errante explorando grandes áreas de campeo, y por tanto tienen el potencial de elegir las mejores.*
- *Existe suficiente conocimiento sobre su biología, fisiología y ecología como para cimentar una aproximación organísmica (Meehan et al. 2004).*
- *Las aves son fácilmente detectables y suficientemente abundantes para obtener buenos tamaños muestrales con esfuerzos de muestreo razonables.*

¿Por qué la Península Ibérica?

- *La Península Ibérica constituye una importante área de invernada para un gran número de especies de aves del Paleártico occidental (Moreau 1972, Perrins 1998). Por esta razón es especialmente interesante analizar la calidad del ambiente invernal que encuentran aquí.*
- *La ecología invernal de aves se ha desarrollado principalmente a latitudes altas, donde los procesos pueden diferir de los que ocurren en el Mediterráneo. Aquí cabe esperar que las aves estén menos limitadas en relación con la temperatura, la adversidad climática y la disponibilidad de alimento (Lack 1954, Fretwell 1972, Newton 1998).*

¿Por qué robledales montanos?

- *Las áreas montañosas ofrecen fuertes gradientes de condiciones ambientales en cortas distancias, debido a la relación adiabática de la temperatura con la altitud, la mayor probabilidad de clima adverso y cobertura de nieve en altitudes altas, y la influencia de la topografía sobre la incidencia del viento y de la radiación solar. Además, las montañas imponen unas condiciones invernales más estrictas a los animales que las zonas bajas.*
- *Trabajar en ecosistemas homogéneos en términos de tipología de hábitat (i.e., bosques) minimiza las variaciones en las respuestas debidas al tipo de hábitat y permite que se manifiesten los determinantes abióticos.*
- *Los robledales (Quercus pyrenaica) de la Sierra de Guadarrama han sido manejados tradicionalmente para la obtención de carbón y pastos para el ganado, lo que ha dado como resultado una gran variedad de bosques en términos de estructura y madurez del arbolado (Costa et al. 1998). Por tanto, aquí es posible analizar el papel de la estructura de la vegetación en la distribución de especies en el contexto de un bosque monoespecífico.*

paisaje forestal [Cap. 2, 3], bosques a

escala regional [Cap. 4, 5, 6], y áreas peninsulares [Cap. 7] (Tabla 1, Figura 3). En todos los capítulos hasta la escala regional [Cap. 1-6], se pone el énfasis en la detección de respuestas a variaciones espaciales sutiles de la temperatura, medidas "in situ" de forma precisa con registradores de datos.

En tercer lugar me pregunto si las especies responderán de forma distinta a la temperatura diurna y nocturna, ya que estas deben estar muy relacionadas con los costes metabólicos de termorregulación en estos periodos, y su significado funcional probablemente sea mayor que el de la temperatura media. Para responder a esta pregunta, comparo la influencia relativa de las temperaturas diurna y nocturna bajo distintos escenarios ecológicos [Cap. 2, 4, 6]. De esta forma pretendo examinar si los promedios son medidas adecuadas del ambiente térmico, o si se necesitan predictores más específicos y con mayor significado funcional para entender las distribuciones de especies.

En cuarto lugar investigo si las aves responden a predictores ambientales que no implican beneficios instantáneos sino diferidos en el tiempo. En concreto analizo la influencia de la temperatura nocturna sobre la distribución diurna [Cap. 4, 5, 6], el efecto de la radiación solar y de la temperatura diurna sobre la selección de dormideros nocturnos [Cap. 3], y la importancia de la altitud como subrogada de las condiciones climatológicas adversas y de la probabilidad de innivación [Cap. 2, 4, 5, 6]. Estos efectos hablarían de una capacidad de previsión de las aves para anticiparse a las adversidades invernales y aumentar así sus probabilidades de supervivencia.

En último lugar trato de entender como la importancia relativa de cada factor ambiental que influye en la distribución de especies varía con el escenario ecológico en el que es considerado, en relación con su significado funcional en un contexto concreto. Este objetivo se aborda comparando la relación de las especies con su ambiente térmico en dos gremios de aves distintos (forrajeadores del suelo [Cap. 4] vs. forrajeadores arbóreos [Cap. 5]), en diferentes periodos del año (invierno vs. estación reproductiva [Cap. 6]), y bajo distintas condiciones climatológicas (clima invernal benigno vs. ola de frío [Cap. 3] e invierno frío vs. invierno más cálido [Cap. 4]). Además me centro en varias decisiones ecológicas (dónde forrajear [Cap. 1, 5], dónde dormir [Cap. 2], y dónde residir [Cap. 3, 4, 5, 6, 7]) analizadas en varias escalas biológicas (desde decisiones individuales [Cap. 1], hasta abundancia de gremios [Cap. 2, 3, 5], riqueza de especies en gremios y comunidades [Cap. 4, 6], anidamiento de comunidades [Cap. 6] y patrones macroecológicos [Cap. 7]). Este esfuerzo analítico tan diverso es concebido para descubrir si el papel del ambiente térmico en la distribución de aves invernantes se puede generalizar a través de diferentes escenarios ecológicos.

Presentación de los capítulos y contribución original de la doctoranda

Esta tesis se basa en siete artículos originales de investigación, cinco de los cuales ya se encuentran publicados en foros internacionales (ver 'Lista de publicaciones originales' en página 13). Aunque cada trabajo es el resultado de una estrecha colaboración entre co-autores, aquí indico únicamente mi contribución.

En el capítulo 1 cuantificamos experimentalmente la importancia relativa de la termorregulación y del riesgo de depredación en la selección de parches de forrajeo por aves forestales invernantes a

escala local. He contribuido a este trabajo en la concepción, diseño y realización del experimento, el análisis de los datos, la discusión de los resultados y la redacción del manuscrito.

En el capítulo 2 analizamos experimentalmente los determinantes de la selección de dormideros invernales por paseriformes forrajeadores arbóreos a escala de paisaje. He contribuido a este trabajo en la concepción, diseño y realización del experimento, el análisis de los datos, la discusión de los resultados y la redacción del manuscrito.

En el capítulo 3, analizamos cómo una ola de frío extremo afecta a la abundancia relativa de aves forrajeadoras arbóreas en invierno, y a su re-distribución a escala de paisaje. He contribuido a este trabajo en la concepción y diseño del estudio, la recolección y el análisis de los datos, la discusión de los resultados y la redacción del manuscrito.

En el capítulo 4, analizamos la influencia relativa del ambiente térmico, el alimento y la estructura del hábitat en la riqueza invernal de especies de aves forestales forrajeadoras en el suelo a escala regional. He contribuido a este trabajo en la concepción y diseño del estudio, la recolección y el análisis de los datos, la discusión de los resultados y la redacción del manuscrito.

En el capítulo 5, analizamos experimentalmente el efecto de la temperatura, el alimento y la estructura del hábitat en la abundancia invernal de aves forestales forrajeadoras arbóreas a escala regional. He contribuido a este trabajo en la concepción, diseño y realización del experimento, el análisis de los datos, la discusión de los resultados y la redacción del manuscrito.

En el capítulo 6, analizamos la influencia de la temperatura en la abundancia de aves terrestres invernantes en la Península Ibérica, y comparamos la efectividad de los modelos bioclimáticos que solo consideran el clima vs. aquellos que también contemplan las preferencias ambientales de las especies. He contribuido a este trabajo en la concepción de la idea, el análisis de los datos, la discusión de los resultados y la redacción del manuscrito.

En cada capítulo se puede encontrar un resumen detallado en castellano junto con el manuscrito original en inglés.

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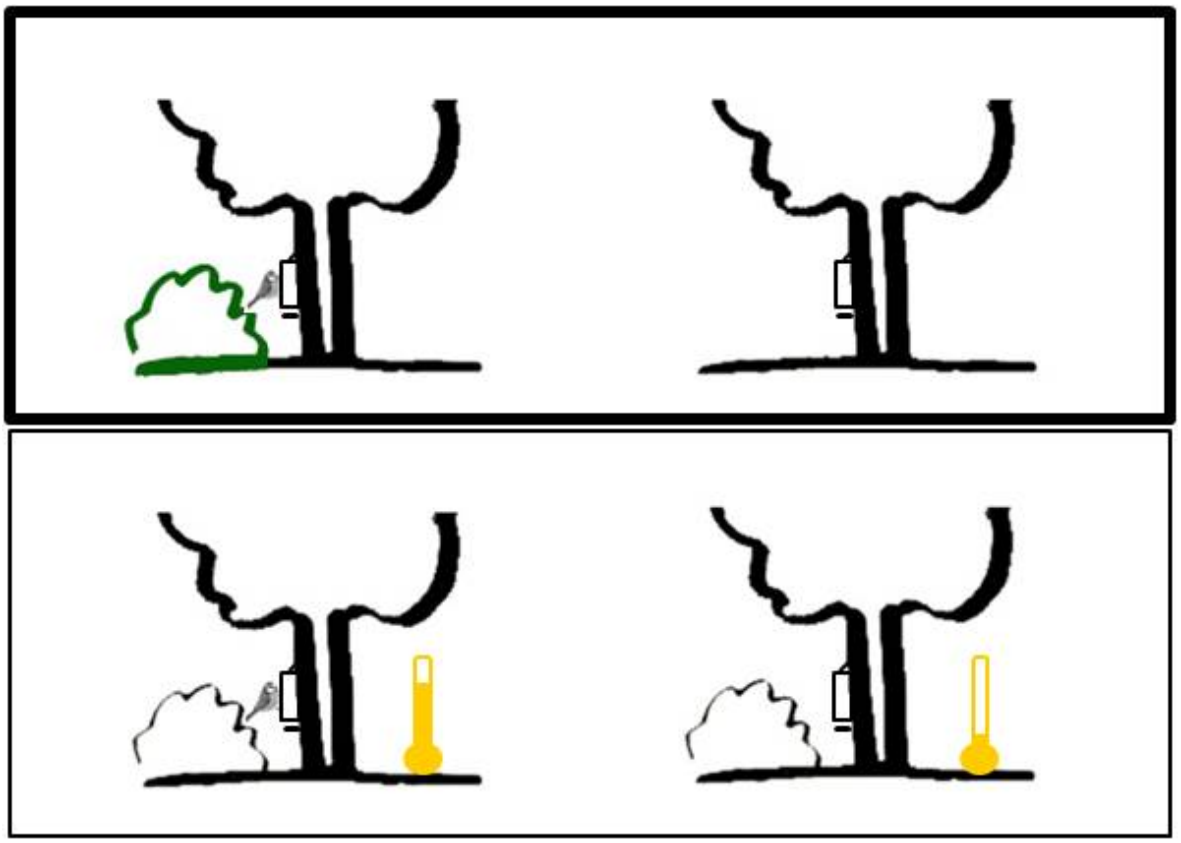
Chapter 1

Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit



Selección de parches de forrajeo en invierno: un equilibrio entre el riesgo de depredación y el beneficio térmico

Objetivo Cuantificar la importancia relativa del coste de termorregulación y el riesgo de depredación en la selección de parches de forrajeo por aves forestales invernantes.

Localización Bosque montano mediterráneo de la Sierra de Guadarrama (escala local).

Métodos Medimos el tiempo que 38 individuos marcados, pertenecientes a cinco especies de paseriformes, pasan forrajeando en comederos artificiales. Situamos los comederos en parches forestales, que varían en distancia a refugios de cobertura vegetal y en exposición a la radiación solar. La temperatura y la iluminación se miden localmente con registradores de datos.

Resultados y discusión Nuestros resultados indican que tanto los beneficios de termorregulación como los costes de depredación influyen en la selección de parches de forrajeo. La influencia de la distancia al refugio (relación negativa) es casi tres veces mayor que la de la temperatura (relación positiva) determinando el tiempo total de forrajeo de un individuo en un parche. La iluminación tiene un efecto inapreciable y no significativo. Este patrón es generalizable entre especies y entre individuos dentro de especie.

Conclusiones Este estudio destaca que el riesgo de depredación latente predomina sobre el beneficio de termorregulación en las decisiones de forrajeo de las aves que invernan en bosques mediterráneos templados.

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Villén-Pérez S, Carrascal LM, Seoane J **(2013)** Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit. *PLoS One* 8(7): e68448

Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit

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Abstract In winter, foraging activity is intended to optimize food search while minimizing both thermoregulation costs and predation risk. Here we quantify the relative importance of thermoregulation and predation in foraging patch selection of woodland birds wintering in a Mediterranean montane forest. Specifically, we account for thermoregulation benefits related to temperature, and predation risk associated with both illumination of the feeding patch and distance to the nearest refuge provided by vegetation. We measured the amount of time that 38 marked individual birds belonging to five small passerine species spent foraging at artificial feeders. Feeders were located in forest patches that vary in distance to protective cover and exposure to sun radiation; temperature and illumination were registered locally by data loggers. Our results support the influence of both thermoregulation benefits and predation costs on feeding patch choice. The influence of distance to refuge (negative relationship) was nearly three times higher than that of temperature (positive relationship) in determining total foraging time spent at a patch. Light intensity had a negligible and no significant effect. This pattern was generalizable among species and individuals within species, and highlights the preponderance of latent predation risk over thermoregulation benefits on foraging decisions of birds wintering in temperate Mediterranean forests.

Keywords *Behavioral thermoregulation · Foraging patch selection · Light intensity · Predation risk · Winter · Woodland birds*

Introduction

In the everyday struggle for life, wintering animals strive to meet the high energy requirements imposed by the season through a suite of behavioral strategies such as feeding during long periods of time and managing heat interchange with their environment [1]. Foraging patch selection can be viewed as a microclimate plus microhabitat selection process, being intended to optimize food search while minimizing both thermoregulation costs and predation risk. The risk of being predated may be related to multiple factors, among which the best known is the distance to a potential refuge against predators [2],[3],[4],[5],[6]. However, there are other factors determining predation risk; for instance, illumination levels highly influence the probabilities of being seen by a potential predator as well as the probabilities of detecting that predator in the surroundings [7],[8],[9].

Three-dimensional habitats such as forests create a complex sun-shade mosaic where each patch has a particular combination of sun incidence (and thus average temperature and light intensity), average food availability, and a given

distance to the closer vegetation refuge from predators. Specifically, sun radiation is predicted to create a conflict in the decision-process of habitat use during foraging, due to the trade-off between energy savings by heating, and predation risk linked to high light intensity [7]. For instance, small passerines at low temperatures around zero ºC reduce metabolic rate by approximately one half when exposed to sun radiation levels of ca. 1000 W/m^2 and low wind speeds [10],[11]. Nevertheless, sun radiation may also increase predation risk through both higher probabilities of being detected by predators and reduced vision of prey due to glare effects [7],[8]. Glare effects may not affect prey and predators in the same way, as predators choose the direction of attack in order to reduce detection by prey [12]. On the other hand, habitat configuration influences the availability of refuges where prey may shelter against predators, and distance to protective cover determines the perception of predation risk. Cover functions as both refuge for prey and as concealment for predators, so birds devote more time to vigilance farther from refuge and prefer to feed near vegetation cover (e.g., [2],[6],[13],[14],[15]).

Habitat structure, thermal, food and predation factors are tightly related in the wild. For instance, temperature is related to food availability through arthropod activation and fruit productivity [16],[17], sun radiation determines both temperature and illumination levels, and it is at the same time influenced by the shade effect of vegetation cover. Due to their high level of correlation, the relative importance of these factors on foraging patch selection has rarely been assessed (but see [7],[18],[19]). Nevertheless, disentangling these intervening effects is crucial to understand the decision-making process of foraging patch selection in wintering animals.

Here we quantify the relative importance of thermoregulation benefits associated with ambient temperature, and predation risk linked to both illumination levels and distance to the nearest refuge, in foraging patch use by wintering forest birds. We analyze the influence of thermal benefits and predation risk in a montane Mediterranean forest of central Spain, with temperatures well below the thermoneutral zone [20],[21]. To attain this goal we made field observations under controlled and comparable situations according to foraging substrate, food access and food quality. We used specially designed feeders located on tree trunks at variable distance to vegetation cover and exposure to sun radiation, in such a manner that distance to cover was not associated with temperature and illumination levels. We registered temperature and light intensity with data loggers located at feeders, and used video recording to measure the cumulative time that individually marked birds exploited each feeder. This manipulative procedure under field conditions controls for the confounding effects of natural food availability, predation risk and thermoregulation benefit on foraging patch selection.

Materials and Methods

Study area and period

The study area was located in central Spain ('El Ventorrillo' field station, a 6 ha research facility of the Museo Nacional de Ciencias Naturales, CSIC; 1460 m a.s.l., 40°45′14"N 04°01′13"W, Sierra de Guadarrama, Madrid province), in a mixed forest dominated by Scots pine *Pinus sylvestris*, chestnut *Castanea sativa*, maples *Acer* spp., poplars *Populus nigra* and Pyrenean oak *Quercus pyrenaica*. Field work was carried out from 1 December 2010 until 10 February 2011. During the study, the average mean diurnal and night temperatures were 4.7 ºC and 1.8 ºC,

respectively (average data from two data loggers –HOBO Pendant– placed in trunks at shade in the field station; see below), with a snowfall frequency of 22% days (data from the neighboring weather station of Navacerrada mountain pass, the nearest meteorological station, located at 1890 m a.s.l., 40º46'50"N 4º00'37"W). Day length at the winter solstice was 8.8 h.

Study species and individual identification

The study species were those belonging to the tree-gleaning guild of the mountainous forests of central Spain that have omnivorous diets [22]: *Cyanistes caeruleus* (Blue Tit, 10-12 g, own data), *Lophophanes cristatus* (Crested Tit, 10-12 g), *Sitta europaea* (Nuthatch, 23-25 g), *Parus major* (Great Tit, 18-20 g) and *Periparus ater* (Coal Tit, 9-10 g). These small-sized species mainly forage in the foliage, twigs and branches of trees, although they can also use the forest floor or trunks as foraging substrates (especially the Nuthatch, the Great Tit and the Crested Tit; [23]). In addition, they are regular exploiters of artificial feeders in the study region (e.g., [6]). Potential predators of small birds in the study area are the Sparrowhawk (*Accipiter nisus*) and the Tawny Owl (*Strix aluco*), although we did not see any of them during the marking or the sampling period. However, predation risk may be higher around feeders than elsewhere if predators are attracted there because of a higher abundance of prey. Birds typically react to predator presence by fleeing to the nearest vegetation cover (see [6],[24] for more details on previous study in the same field station).

In order to trap birds for individual identification, five rectangular funnel traps (40 × 40 × 60 cm) were placed all around the study area, 50–100 m apart and hanging from branches 1.5 m above the ground, from 1 December 2010 to 20 January 2011. This kind of trap is especially efficient at capturing tit species and can be used under adverse weather conditions [25]. Funnel traps were permanently baited with two cylindrical feeders, hanging from the trap roof, which contained husked peanuts. A translucent plastic sheet covered the roof of the traps to prevent birds from getting wet on rainy or snowy days. The escape doors of the traps remained opened on non-capture days, so birds could use the peanuts as a supplementary food source, but they were closed during the capture days from dawn to dusk. Trapping was conducted on 13 days from 8:30 to 17:30 hours GMT. On capture days, traps were inspected every 30–45 min. Captured birds were given unique color rings and released as quickly as possible after manipulation (handling time: 2-10 min). The Spanish agency in charge of environmental policy and animal welfare of Madrid (Consejería de Medio Ambiente, Comunidad de Madrid) approved the capture and study of birds (permit number 10/479348.9/10).

We marked a total of 60 individuals: 10 nuthatches, 17 great tits, 12 blue tits, 12 crested tits and 11 coal tits. Birds were recaptured an average of 6.45 times. Recaptures become steadily more frequent along the capture period, until reaching almost 100% of total captures in the five studied species.

Experimental set up

Within the study area, ten feeders were established at least 20 m apart from one another. Each feeder was filled with husked peanuts and suspended from a nail 1.5 m above ground on thick trunks of pines or deciduous trees. Feeders were metallic cylinders (25 x 5 cm) made from a 4.8 mm mesh net allowing birds access to food. Feeders never ran out of peanuts during the study period (so birds could not find them empty). The feeders were located at least 10 m away from the positions where the funnel traps were located, so feeder choice by foraging birds could not be linked with previous

experience related to predation risk due to bird trapping.

We carefully selected the location of the ten experimental feeders within the natural forest environment according to a broad variation in temperature, light intensity and distance to the nearest vegetation cover considering our previous experience in the study area (see Appendix 1).

Air temperature and light intensity at each feeder was assessed with one data logger (HOBO Pendant, Onset; 58 x 33 x 23 mm) located at the lower end of each feeder. In order to standardize the registering of light intensity, the light sensor of the logger was pointed to the ground and a grey plastic plate of 60 x 40 mm was placed parallel to it and 2 cm below the light sensor. Thus, all loggers recorded the reflected light from same material of identical reflection properties. Data loggers recorded air temperature (measured in ºC) and light intensity (measured in lux, lumens / m^2) every minute during the sampling period. For each sampling day, 600 measurements of temperature and light intensity were obtained from 7:30 to 17:30 hours GMT. Data on temperature and light intensity during daytime at each feeder were averaged across the 14 days of sampling to characterize the environmental idiosyncrasy of feeders. Differences among feeding patches in average temperature ranged up to 3.7 ºC (from 4.5 to 8.2 ºC), while differences in average light intensity reached 9598 lux (from 299 to 9897 lux).

Two situations were selected to simulate low and high-predation risk locations according to the distance to protective vegetation cover, considered here as needles, small branches, twigs of bushes, and tree regrowth (< 1 cm diameter) that could offer refuge to the birds when attacked by a predator. The low risk position ('near') was defined as at <0.4 m from the nearest vegetation cover, and the high-risk position ('far') as at >3 m from cover. Distance to cover is clearly associated with perceived predation risk, as previously found in similar studies reporting longer distances of escape to safe refuges, increases in vigilance rate, and decreases in average times spent at feeders per foraging bout in 'far' locations (e.g., [26] and references therein; [6],[13],[14],[15]). We selected six feeders 'near' and four 'far' from refuge, that cluster into two relatively homogeneous levels when considering the logarithm of their distances (ln distance to refuge in 'near' feeders: mean = 0.2, sd = 0.12; 'far' feeders: mean = 1.6, sd = 0.23;-distance to refuge is considered on its logarithm according to the accelerated nature of flight movement while taking off). We made this unbalanced selection as the best *a priori* solution to uncouple the natural variation of distances and both temperature and light intensity at each feeder. Thus, the covariation between distance to vegetation refuge ('near' vs. 'far') and both average temperature and luminosity were minimal (temperature: $F_{1,8} = 0.24$, $p = 0.635$, $R^2 = 0.03$; luminosity in logarithm: $F_{1,8} = 0.34$, $p = 0.575$, $R^2 = 0.04$; n = 10 feeders using data in the Appendix 1). A high correlation between temperature and luminosity was unavoidable when considering average figures for each feeder, as both variables are naturally dependent on sun radiation ($R^2 = 0.84$). This correlation imposes a conflictive demand between the beneficial effects of temperature and the deleterious effects of luminosity.

Feeder use by birds

Field work on feeder use was carried out from 21 January to 10 February 2011, considering only data for 14 cloudless, anticyclonic and near windless days (average wind speed of 3 m/s in the nearest weather station, Navacerrada mountain pass, located 4 km away from El Ventorrillo at 1890 m a.s.l. in an open,

windier, mountain area; 40º46'50"N 4º00'37"W). Moreover, the influence of wind is considered to be negligible in our study design because feeders were located at low heights inside a dense, mature, forest (i.e., other trees provided shelter against wind, determining that wind direction was probably random in our study area). Average day length was 10 h 11 min and average potential sun radiation at zenith was 609 W/m^2 during the sampling period. Artificial feeders were settled in the 10 study locations 32 days prior to the beginning of the sampling period, from 20 December 2010 to 20 January 2011. Considering this pre-feeding period, and the fact that the funnel traps also contained similar feeders with husked peanuts, we assumed the feeder setup was easily identifiable as a food source for birds.

We quantified the cumulative time foraging at each one of the 10 feeders by video monitoring (Appendix 2). A digital zoom video camera (Sanyo VPC-GH1 and Toshiba Gigashot GSC-K80) mounted on a tripod was placed at a distance of 1-2 m from each one of the 10 feeders, recording the number and duration of visits each individual bird made at each feeder. Frame rates were set at 21 fps. Color rings were clearly visible on video recordings, so it was possible to identify individual birds. The sampling period spanned from 7:30 to 17:30 hours GMT. Four video cameras were used in the sampling, rotating among the 10 of feeders, according to an *a priori* time schedule that tried to sample the feeders with a complete overlap of days and hours. Each feeder was videotaped for an average of 3.7 hours during a sampling day, and the average sampling effort was 37 h 42 min per feeder (range: 23 h 22 min / 53 h 26 min). Thus, each feeder was sampled approximately 23.1% of diurnal time available.

We used media player software (MicroSoft® Windows Media Player 12 and VideoLAN VLC) to watch the video recordings and to measure the amount of time each individual bird spent foraging on each feeder.

The total number of visits to feeders was 900, with an average number of 23.7 visits that an individual bird made to the 10 feeders (range: 12-54), and an average time of stay per foraging bout of 58.9 seconds. The average number of different feeders used by each bird was 4.6, ranging between two and nine feeders. Some feeders were only visited on 11 occasions throughout the study period, while others accounted for more than 150 foraging bouts (a maximum of 276). The frequency of visits was significantly related to the cumulative time spent at each feeder throughout the sampling period ($R^2 = 0.83$, $p << 0.001$). However, we chose the cumulative time spent at each feeder by each individual bird as the response variable, because it is a more precise measure of the foraging intensity at each feeder location as it includes the duration of all foraging bouts. Cumulative time spent at each feeder was standardized by dividing that amount of time by the recording time at each feeder, and it was expressed in seconds per 10 hours of recording.

We work with the cumulative time spent foraging at each feeder instead of the duration of each foraging bout because (1) we are interested in analyzing habitat use by a resident population of birds throughout the winter, (2) our study is not aimed at analyzing instantaneous decisions on how long to forage according with state-dependent conditions (e.g., internal reserves, satiation, time to dusk, etc.), and (3) the lack of feeding activity at some feeders by some birds is ecologically very relevant.

Data analyses

Although many ringed birds were detected in video recordings, only those

individual birds for which at least 10 visits to feeders were obtained were included in the statistical analyses. We used this threshold considering that a minimum of 10 visits would be necessary for a bird to be able to forage at least once at each feeder. The final sample size was 38 different birds: 10 nuthatches, 6 great tits, 6 blue tits, 5 crested tits and 11 coal tits.

A General Linear Mixed Model was applied to analyze the cumulative time spent feeding at each feeder (response variable) by 38 different individual birds (i.e., a data matrix with cumulative times at ten feeders by 38 focal birds). Bird identity (BIRD) was considered as a random factor, species (SPECIES) and distance to cover (DISTANCE) as fixed factors, and average diurnal temperature (T) and average light intensity (LI) at feeders as covariates. Bird identity was nested within the corresponding species (i.e., differences among species were tested considering the individual bird as the sample unit instead of the foraging stays at each feeder). The mean square (MS) and the degrees of freedom (df) of the error terms were estimated following Satterthwaite's method, which finds the linear combinations of sources of random variation that serve as appropriate error terms for testing the significance of the respective effect of interest. We also tested for parallelism in the relationships between time spent at feeders and temperature (DISTANCE*T) or light intensity (DISTANCE*LI) across the two levels of distance. The cumulative time spent foraging at feeders and light intensity were transformed logarithmically prior to data analyses. Homoscedasticity and normality of residuals of the General Linear Mixed Model were checked and they did not deviate from the canonical assumptions. Data were analyzed using StatSoft's Statistica 10.0 (StatSoft Inc, Tulsa, Oklahoma).

Results

The General Linear Mixed Model (all effects: $F_{151,228} = 1.41$, $p = 0.010$, 48.2% of the variance accounted for; Table 1) shows that distance to cover (partial regression coefficient, $\beta = -0.352$) and temperature ($\beta = 0.266$) had significant effects on feeding intensity in the ten foraging patches (Figure 1). Birds spent more time feeding at 'near' (mean $\pm$ se, 47.8 $\pm$ 5.8 s / 10 h, n=38 birds) than at 'far' feeders (12.0 $\pm$ 2.6 s / 10 h), and at five warmer (48.6 $\pm$ 6.6 s / 10 h) than at.

Table 1. Sources of variation in foraging-patch use. General Linear Mixed Model of the cumulative time feeding at 10 foraging patches, by wintering birds (38 different individual birds belonging to 5 species) in a mixed montane forest of central Spain, considering bird identity (individual, random factor), species and distance to cover (fixed factors), and average diurnal temperature and average light intensity at feeders (covariates). Partial η^2: partial eta-squared measuring the magnitude effects of predictor terms.

Effect	SS	Partial η^2	df	F	p
Species	25.6	0.14	4, 33	1.40	0.257
Individual within species	151.5	0.16	33, 228	1.34	0.115
Temperature (ºC)	24.4	0.25	1, 37	12.34	0.001
Ln light intensity (lux)	3.8	0.03	1, 37	1.33	0.256
Distance to cover ('near'-'far')	179.3	0.66	1, 37	73.08	< 0.001
Individual x Temperature	73.2	0.09	37, 228	0.58	0.977
Individual x Ln light intensity	106.1	0.12	37, 228	0.83	0.741
Individual x Distance to cover	90.8	0.10	37, 228	0.71	0.890

five colder feeders (18.4 ± 3.8 s / 10 h). Neither the species nor the individual birds and the interaction terms birds x predictors reached significance (temperature, light intensity and distance to cover), which means that the described pattern of feeder use is generalizable among species and individuals within species. Moreover, the interaction terms between distance to cover and temperature ($F_{1,74}$ = 0.302, p = 0.584) or distance x light intensity ($F_{1,74}$ = 0.318, p = 0.574) were also non-significant, showing that the positive influence of temperature, or the lack of effect of illumination, did not change between near and far from vegetation cover. Distance to cover, which may provide refuge against predators, was the predictor variable with the highest magnitude effect (partial η^2 = 0.66), followed by temperature at feeders (0.25).

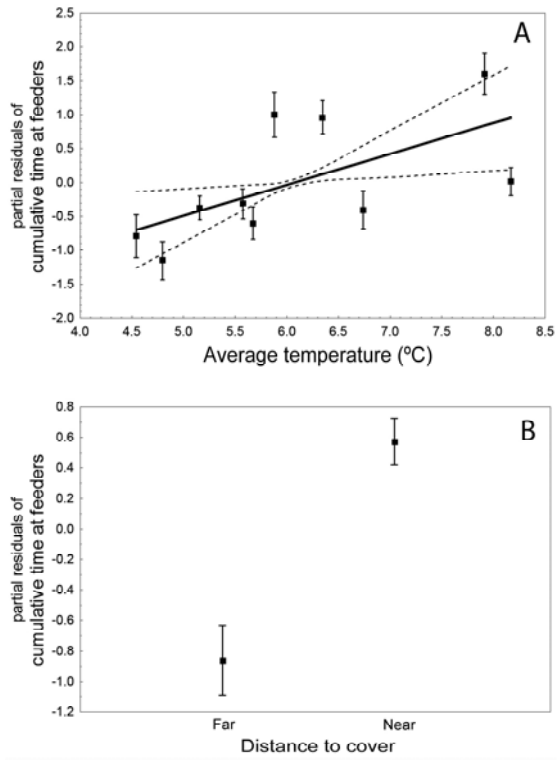

Figure 1. Influence of temperature and distance to cover on foraging patch use. Relationship between the cumulative time spent at each feeder by forest birds and (A) the average temperature at feeders along the study winter period (20 January-10 February 2011) and (B) the distance to the closest vegetation refuge against predators, in a mixed montane forest of central Spain. Figures represent average and standard error of partial residuals from a General Linear Mixed Model on ln seconds of stay / 10 sampling hours (Table 1) at all ten feeders (A) and at six far and four close feeders (B). Solid line represents linear fitting equation and dashed lines regression bands at 0.95 confidence level. Sample size is 38 individuals of five bird species: *Cyanistes caeruleus, Lophophanes cristatus, Periparus ater, Parus major* and *Sitta europaea.*

Therefore, the influence of distance to refuge was 2.6 times higher than that of temperature in determining the foraging intensity at feeding patches, while light intensity had a negligible and no significant effect.

Discussion

Wintering birds were able to identify small variations in temperature across foraging patches, devoting more time to relatively warm patches and likely reducing the thermoregulation expenditure while searching for food (Figure 1A). Birds also perceived the potential risk of being predated, spending more time foraging at safer patches with a close refuge available to escape from predators (Figure 1B). Noticeably, minimizing predation risk was much more important than reducing thermoregulation metabolic costs in these Mediterranean forests of relatively mild winter climate.

Wintering birds benefit from foraging at patches with higher environmental temperature where the costs of thermoregulation are reduced. Our results support this metabolic benefit in a forest scenario, where the sun-shade mosaic generates a broad spatial micro-variation in temperature [7],[27],[28],[29]. The energy saved by selecting the warmest foraging sites may be even more relevant when considering its cumulative effect on the long-term winter energy balance of these small birds, considering that they spend most of their winter daytime

foraging under temperatures well below their thermoneutral zone ([20],[21]; 202 consecutive days below 20ºC in winter 2010-2011 at Navacerrada mountain pass weather station; www.aemet.es).

In addition, birds that escape from predators by seeking shelter in dense vegetation minimize the risk of being predated by foraging close to vegetation cover [2],[4],[6],[30], and spend more time vigilant (even at large-habitat scale) in more fragmented or opened managed forest [31],[32]. Predation is thus perceived as a permanent potential risk and, as such, it exerts a continuous effect on the behavior of birds [33]. Moreover, predation is an unpredictable risk of 'all or nothing' consequences: a sole successful event of predation will be lethal, increasing this risk with distance to shelter. Therefore, small differences in flight time and distance to a safe refuge against predators while foraging have a paramount influence on microhabitat use. In our study, the average distances to the nearest refuge of 'close' and 'far' feeders were 0.3 and 4.3 m, corresponding approximately to 0.5 and 2.1 seconds of escape flights [34]. Our results show that birds follow anti-predator strategies steadily, even in the apparent absence of predators, as no predator attacks were observed during the ca. 420 hours devoted to fieldwork.

The effect of predation risk associated with the distance to dense cover was 2.6 times greater than that of the thermoregulation benefit associated with temperature (compare partial-η^2 in Table 1). The hierarchical prioritization of predator avoidance over reduction of thermoregulation cost brings a sub-optimal exploitation of the thermal environment, as the time spent in patches with the lowest thermoregulation expenditure is not maximized [2],[7],[35],[36],[37]. An optimal exploitation of the thermal environment may gain importance in colder environments, and thus the relative importance of predation and thermoregulation is prone to change with the environment. In Mediterranean forests, in spite of the uncertainty associated with predation, betting on survival against predators preponderates over the tangible benefits of reducing metabolic costs.

We predicted that sun radiation would promote a conflictive demand between the benefits of sunbathing and predation risk associated with visibility. Contrary to our expectations, we found no effect of illumination determining the time that a forest patch is exploited. This contrast with some studies that relate luminance with both the risk of being detected by a predator and the difficulties the glare poses to detect predators [7],[8],[9],[38].

All species and all individuals within species followed a similar decision-making process in habitat use (see species, individual and interaction terms in Table 1). Therefore, the preponderance of avoiding predation over facilitating the maintenance of a positive energy balance is generalizable for small passerines facing the winter season, at least in relatively mild temperate Mediterranean forests. Thus, variations in the predation risk – thermoregulation trade-off would probably be related to the abiotic scenario rather than to the species involved. For this reason it would be interesting to test this trade-off in more restrictive scenarios according to winter climate.

In conclusion, wintering birds are able to identify and exploit subtle thermal variations in their foraging environment, minimizing the metabolic costs of thermoregulation while searching for food. Foraging intensity also depends on vegetation characteristics around feeding patches that define potential refuges against predators. The benefits of behavioral thermoregulation are direct, predictable and instantaneously perceived, but its quantitative importance is almost three times lower than that of reducing

predation risk, which has an indirect and unpredictable effect.

Acknowledgements

This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Education and Science. The Biological Station 'El Ventorrillo' provided us with the space and logistical support, the Universidad Autónoma de Madrid (Unidad de Recursos Audiovisuales y Multimedia) and Óscar Seoane (Invisible Producciones Audiovisuales) provided some video cameras and technical material. We also thank Belén Rueda for help with watching recorded videos, Jennie Carr for helpful comments on a first draft of the manuscript and C. Jasinski for improving the English of the manuscript.

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Supporting Information

Appendix 1. Characteristics of the ten experimental feeders.

Appendix 2. Feeding time (seconds of feeder use per 10 hours of recording time) spent by individual birds at each feeder

Appendix 3 (NOT PUBLISHED). An example of the videos obtained and utilized in this study.

Appendix 1.

Characteristics of the ten experimental feeders. Temperature and light intensity refer to those registered during the 14 sampling days. The dashed line divides feeders included in 'near' and 'far' categories. Feeding time and visits to feeders are cumulative numbers for all 38 birds, measured in seconds of feeder use and number of visits per 10 hours of recording time, respectively.

Feeder	Temperature (ºC)	Light intensity (lux)	Distance to cover (m)	Recording time (h:min)	Foraging time (s /10 h)	Visits to feeders (# / 10 h)	# Species	# Individuals
1	4.8	781	0.1	44:05	772	18	5	22
2	4.5	299	0.3	42:11	1769	26	5	23
3	7.9	6645	0.3	46:11	3814	64	5	40
4	6.7	3685	0.3	53:26	916	17	5	24
5	5.9	2790	0.4	36:55	2997	56	5	35
6	5.7	2963	0.4	37:03	591	16	5	25
7	6.3	2453	3.2	41:07	1156	24	5	27
8	8.2	9910	3.4	26:17	306	6	3	11
9	5.6	2720	4.0	23:22	242	5	1	6
10	5.2	1000	6.5	26:24	116	5	3	4

Appendix 2.

Feeding time (seconds of feeder use per 10 hours of recording time) spent by individual birds at each feeder (see characteristics in Appendix 1). Only 38 individual birds for which at least 10 visits to feeders were obtained are shown (i.e., those included in the statistical analyses). Individuals are numbered within specie. Cc: *Cyanistes caeruleus*, Lc: *Lophophanes cristatus*, Se: *Sitta europaea*, Pm: *Parus major*, Pa: *Periparus ater.*

Individual	Feeder #	Foraging time (s / 10 h)
Cc-1	1	0
Cc-2	1	0
Cc-3	1	36.3
Cc-4	1	2.3
Cc-5	1	123.2
Cc-6	1	0
Lc-1	1	0
Lc-2	1	0
Lc-3	1	72.4
Lc-4	1	0
Lc-5	1	0
Pa-1	1	0.7
Pa-2	1	44.5
Pa-3	1	0
Pa-4	1	0
Pa-5	1	0
Pa-6	1	0
Pa-7	1	3.9
Pa-8	1	3.9
Pa-9	1	1.4
Pa-10	1	22.2
Pa-11	1	0.5
Pm-1	1	47.9
Pm-2	1	0
Pm-3	1	9.8
Pm-4	1	62.8
Pm-5	1	39.5
Pm-6	1	0
Se-1	1	90
Se-2	1	5.4
Se-3	1	0
Se-4	1	0
Se-5	1	0
Se-6	1	0
Se-7	1	159.5
Se-8	1	0
Se-9	1	17.7
Se-10	1	28.6
Cc-1	2	0
Cc-2	2	0
Cc-3	2	0
Cc-4	2	23.5
Cc-5	2	373.6
Cc-6	2	80.1
Lc-1	2	0
Lc-2	2	0
Lc-3	2	152.2
Lc-4	2	14.9
Lc-5	2	14.9
Pa-1	2	137
Pa-2	2	0
Pa-3	2	0
Pa-4	2	0
Pa-5	2	0
Pa-6	2	0
Pa-7	2	0
Pa-8	2	0
Pa-9	2	0
Pa-10	2	0
Pa-11	2	0
Pm-1	2	127.3
Pm-2	2	0
Pm-3	2	84.1
Pm-4	2	315.3
Pm-5	2	295.8
Pm-6	2	0
Se-1	2	32.9
Se-2	2	7.3
Se-3	2	39.1
Se-4	2	0
Se-5	2	8.8
Se-6	2	0
Se-7	2	26.1
Se-8	2	0
Se-9	2	27.3
Se-10	2	8.3
Cc-1	3	185.8

Cc-2	3	288.2
Cc-3	3	143.8
Cc-4	3	60.6
Cc-5	3	0
Cc-6	3	525.8
Lc-1	3	200.7
Lc-2	3	51.1
Lc-3	3	49.2
Lc-4	3	188.2
Lc-5	3	118.2
Pa-1	3	0
Pa-2	3	45.5
Pa-3	3	31.8
Pa-4	3	99.4
Pa-5	3	57.8
Pa-6	3	133
Pa-7	3	55.4
Pa-8	3	69.1
Pa-9	3	37
Pa-10	3	105.9
Pa-11	3	74.9
Pm-1	3	235.4
Pm-2	3	268.7
Pm-3	3	450
Pm-4	3	0
Pm-5	3	0
Pm-6	3	103.5
Se-1	3	13.4
Se-2	3	10.8
Se-3	3	24.7
Se-4	3	0
Se-5	3	33.8
Se-6	3	0
Se-7	3	0
Se-8	3	6.7
Se-9	3	68.6
Se-10	3	91.4
Cc-1	4	57.5
Cc-2	4	139.8
Cc-3	4	0
Cc-4	4	7.1
Cc-5	4	0
Cc-6	4	39.7
Lc-1	4	0
Lc-2	4	0
Lc-3	4	0
Lc-4	4	37.8
Lc-5	4	0
Pa-1	4	0
Pa-2	4	0
Pa-3	4	0
Pa-4	4	0
Pa-5	4	2.2
Pa-6	4	0
Pa-7	4	0
Pa-8	4	0
Pa-9	4	0
Pa-10	4	0
Pa-11	4	0
Pm-1	4	90.8
Pm-2	4	21.1
Pm-3	4	10.3
Pm-4	4	0
Pm-5	4	0
Pm-6	4	101.6
Se-1	4	1.5
Se-2	4	2.8
Se-3	4	9.2
Se-4	4	169.6
Se-5	4	16.3
Se-6	4	105
Se-7	4	3
Se-8	4	56
Se-9	4	25.8
Se-10	4	44
Cc-1	5	24.7
Cc-2	5	127.9
Cc-3	5	190.7
Cc-4	5	391.2
Cc-5	5	39.8
Cc-6	5	109.7
Lc-1	5	79.4
Lc-2	5	160.7
Lc-3	5	30.9
Lc-4	5	126.8
Lc-5	5	106.5
Pa-1	5	0
Pa-2	5	64.2
Pa-3	5	31.7
Pa-4	5	117.3
Pa-5	5	197.8
Pa-6	5	102.7

Pa-7	5	5.4
Pa-8	5	6.8
Pa-9	5	137.4
Pa-10	5	83.2
Pa-11	5	36.8
Pm-1	5	137.6
Pm-2	5	137.6
Pm-3	5	375.2
Pm-4	5	0
Pm-5	5	0
Pm-6	5	0
Se-1	5	34.4
Se-2	5	1.9
Se-3	5	0
Se-4	5	0
Se-5	5	0
Se-6	5	0
Se-7	5	92.9
Se-8	5	0
Se-9	5	46.1
Se-10	5	0
Cc-1	6	53.7
Cc-2	6	0
Cc-3	6	27.5
Cc-4	6	0
Cc-5	6	4.3
Cc-6	6	190.5
Lc-1	6	0
Lc-2	6	0
Lc-3	6	0
Lc-4	6	15.9
Lc-5	6	30.5
Pa-1	6	0
Pa-2	6	0
Pa-3	6	44
Pa-4	6	35.6
Pa-5	6	0
Pa-6	6	0
Pa-7	6	5.9
Pa-8	6	0
Pa-9	6	0
Pa-10	6	0
Pa-11	6	0
Pm-1	6	8.1
Pm-2	6	0
Pm-3	6	10.3
Pm-4	6	0
Pm-5	6	0
Pm-6	6	24.6
Se-1	6	4
Se-2	6	13
Se-3	6	25.1
Se-4	6	0
Se-5	6	51
Se-6	6	20.8
Se-7	6	0
Se-8	6	25.9
Se-9	6	0
Se-10	6	0
Cc-1	7	211.8
Cc-2	7	0
Cc-3	7	9.2
Cc-4	7	10
Cc-5	7	0
Cc-6	7	71.5
Lc-1	7	0
Lc-2	7	0
Lc-3	7	0
Lc-4	7	24.1
Lc-5	7	19.9
Pa-1	7	0
Pa-2	7	0
Pa-3	7	18.5
Pa-4	7	10.2
Pa-5	7	7.3
Pa-6	7	0
Pa-7	7	13.4
Pa-8	7	11.7
Pa-9	7	0.5
Pa-10	7	0
Pa-11	7	31.1
Pm-1	7	49.6
Pm-2	7	0
Pm-3	7	8.3
Pm-4	7	0
Pm-5	7	0
Pm-6	7	0
Se-1	7	48.6
Se-2	7	12.6
Se-3	7	100
Se-4	7	0
Se-5	7	268.7
Se-6	7	0
Se-7	7	32.1

Se-8	7	27
Se-9	7	55
Se-10	7	114.8
Cc-1	8	0
Cc-2	8	40.7
Cc-3	8	164
Cc-4	8	11.4
Cc-5	8	0
Cc-6	8	0
Lc-1	8	0
Lc-2	8	0
Lc-3	8	0
Lc-4	8	0
Lc-5	8	0
Pa-1	8	24.7
Pa-2	8	0
Pa-3	8	0
Pa-4	8	0
Pa-5	8	0
Pa-6	8	0
Pa-7	8	0
Pa-8	8	0
Pa-9	8	0
Pa-10	8	0
Pa-11	8	0
Pm-1	8	0
Pm-2	8	0
Pm-3	8	0
Pm-4	8	0
Pm-5	8	0
Pm-6	8	0
Se-1	8	8
Se-2	8	0
Se-3	8	26.3
Se-4	8	0
Se-5	8	0
Se-6	8	0
Se-7	8	10.7
Se-8	8	0
Se-9	8	14.5
Se-10	8	6.1
Cc-1	9	0
Cc-2	9	0
Cc-3	9	0
Cc-4	9	0
Cc-5	9	0
Cc-6	9	0
Lc-1	9	0
Lc-2	9	0
Lc-3	9	0
Lc-4	9	0
Lc-5	9	0
Pa-1	9	0
Pa-2	9	0
Pa-3	9	0
Pa-4	9	0
Pa-5	9	0
Pa-6	9	0
Pa-7	9	0
Pa-8	9	0
Pa-9	9	0
Pa-10	9	0
Pa-11	9	0
Pm-1	9	0
Pm-2	9	0
Pm-3	9	0
Pm-4	9	0
Pm-5	9	0
Pm-6	9	0
Se-1	9	12
Se-2	9	32.5
Se-3	9	0
Se-4	9	125
Se-5	9	0
Se-6	9	45.4
Se-7	9	21.8
Se-8	9	0
Se-9	9	5.1
Se-10	9	0
Cc-1	10	0
Cc-2	10	0
Cc-3	10	0
Cc-4	10	0
Cc-5	10	0
Cc-6	10	3.8
Lc-1	10	0
Lc-2	10	0
Lc-3	10	0
Lc-4	10	0
Lc-5	10	0
Pa-1	10	0
Pa-2	10	0

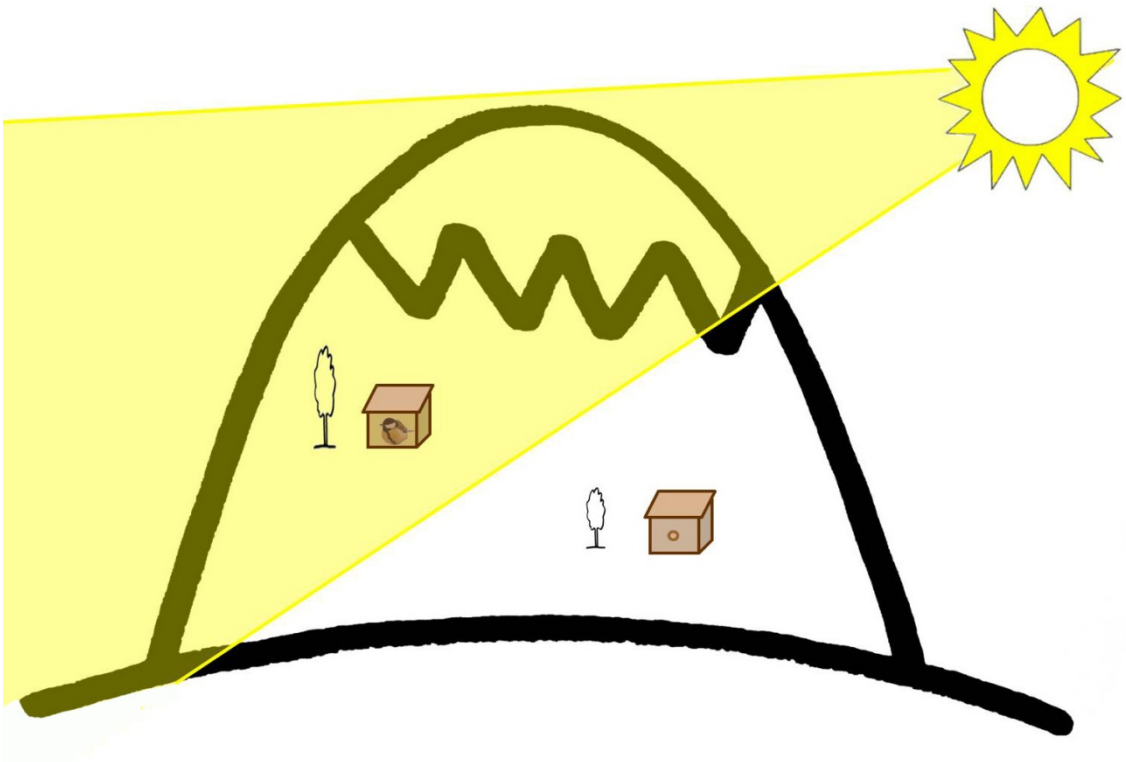
Pa-3	10	0	Pa-7	10	0
Pa-4	10	0	Pa-8	10	0
Pa-5	10	0			
Pa-6	10	0			

Appendix 3 (NOT PUBLISHED).

An example of the videos obtained and utilized in this study for sampling the total foraging time of marked individuals can be found in the following URL:
http://avesbiodiv.mncn.csic.es/saravillen/videotesisvillen.avi
This video comprises the visits of three different individuals to feeder number 3: *Sitta europaea* (individual Blue/-) staying 10 seconds, *Cyanistes caeruleus* (Red/-) staying 35 seconds, and *Parus cristatus* (Yellow/Yellow) staying 11 seconds.

Chapter 2

Wintering forest birds roost in areas of higher sun radiation



Las aves forestales invernantes duermen en áreas de mayor radiación solar

Objetivo Analizar los determinantes ambientales de la selección de dormideros por paseriformes invernantes en un área con una gran variación de altitud e insolación. Nuestra hipótesis es que en latitudes templadas de clima invernal frio, las aves dormirán en las zonas más bajas, más cálidas y más insoladas, para minimizar los gastos de termorregulación durante el periodo de descanso y mejorar las condiciones de forrajeo antes y después de este periodo.

Localización Robledal montano mediterráneo de la Sierra de Guadarrama (escala de paisaje).

Métodos Estudiamos la ocupación nocturna de 159 cajas nido (dormideros de condiciones controladas idénticas) a través de la presencia de excrementos en ellas. Utilizamos sistemas de información geográfica (SIG) para cuantificar la radiación solar potencial recibida en los alrededores de cada caja, y registradores de temperatura para medir la variación de la temperatura en la zona.

Resultados y discusión Las aves prefieren dormir en las zonas forestales más insoladas, donde se alarga el periodo con luz suficiente para el forrajeo y se minimizan los costes de termorregulación diurnos. Estas especies también prefieren las zonas con arbolado de mayor altura, en relación con sus preferencias de forrajeo. Otras variables ambientales no ejercen ninguna influencia sobre la selección de dormideros nocturnos.

Conclusiones En este trabajo mostramos por primera vez la influencia de la radiación solar sobre la selección de dormideros nocturnos en aves invernantes, resaltando la importancia de considerar el espacio térmico en el manejo forestal. Para mejorar el hábitat invernal de las aves de estos robledales mediterráneos se deberán preservar aquellos bosques de arbolado maduro más expuestos a la radiación solar.

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Villén-Pérez S, Carrascal LM, Gordo O **(2013)** Wintering forest birds roost in areas of higher sun radiation. *European Journal of Wildlife Research* DOI 10.1007/s10344-013-0750-7

Wintering forest birds roost in areas of higher sun radiation

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Abstract We analyze environmental determinants of roost site selection by tree gleaning passerines wintering in a Mediterranean montane oakwood at a craggy area of high variation in altitude and hill-shading pattern. We hypothesize that in temperate latitudes of cold winter climate, birds should spend the night in areas of low altitudes, higher temperatures, and higher solar radiation in order to minimize thermoregulation costs during resting time and to improve foraging conditions just before and after roosting. We study night occupation of woodland locations by the presence of feces in 159 wooden nest boxes (i.e., under identical controlled roosting situations). We employ GIS methods to quantify solar radiation at each location surrounding the nest boxes and data loggers to measure air temperature in the field. Birds prefer to roost in forest patches with higher solar radiation, where the period of light available for foraging is extended and thermoregulation costs during daytime are minimized. They also selected woodland patches with taller trees, a pattern consistent with their foraging preferences for trunks and branches. Other environmental variables played a negligible role in determining the selection of roost sites. Here, we show, for the first time, the importance of sun radiation determining where to spend the night in wintering birds and call attention on considering the thermal space in forest management. Forest management should preserve woodland patches with taller trees more exposed to solar radiation to enhance winter habitat suitability for birds in these Mediterranean oakwoods.

Keywords: *Nest boxes · Night roosting · Sun radiation · Temperature · Winter · Woodland birds*

Introduction

Winter is the most severe season for small passerines of temperate and boreal latitudes. Long and cold winter nights become the most stringent period of the day, when birds have to cope with temperatures well below their thermoneutral zone (Calder and King 1974) while fasting for many hours. Thus, birds have developed several behavioral strategies in order to minimize thermoregulation costs and to ensure winter survival (Mayer et al. 1982; Swanson 1993; Carey 1996; McKechnie and Lovegrove 2002). Roost site selection is an important decision when facing harsh conditions of winter nights (Pinowski et al. 2006; Coombs et al. 2010, Grüebler et al. 2013). Birds select warmer forest areas and roost sites to reduce metabolic expenditure during resting time (Virkkala 2004; Velky 2006; Velky et al. 2010, Zabala et al. 2012), and they can further reduce the rate of heat loss by radiation and wind-forced convection by sheltering in dense vegetation (Lustick and Kelty 1979; Buttemer 1985; Webb and Rogers 1988), winter nests (Buttemer et al. 1987), tree cavities (Kendeigh 1961; Coombs et al. 2010), or artificial nest boxes (Pinowski et al. 2006).

After long fasting and energy-consuming winter nights, when fat reserves

are at minimum level, finding food in the shortest possible time is also essential for survival (Houston and McNamara 1993). In addition, a successful and late foraging at the end of the day may be important in order to accumulate enough fat reserves to get through the following night, especially in those days of harsh weather conditions (Blem 1990; McNamara et al. 1994; Polo et al. 2007).

The environmental and foraging conditions of birds during the previous afternoon and the following morning might be determined by multiple factors. Harsh winter weather (e.g., snowstorms and wind) may make difficult or even impede food searching, and snow and ice can cover food resources limiting their availability, with dramatic consequences for fasting birds. Both unpredictable harsh weather and snow cover are strongly and directly related with altitude, and therefore, birds generally prefer to overwinter in lowlands (e.g., Herbers et al. 2004; Senar and Borrás 2004). Temperature exerts a prominent role on bird metabolism below the critical minimum (usually around 20 ºC for small passerine; Kendeigh et al. 1977) and is likely to improve the quality of the foraging environment (Robinson et al. 2007; Cresswell et al. 2009), so birds are expected to distribute accordingly, selecting areas with higher temperatures during winter at different spatial scales, all other things being equal (e.g., Root 1988; Meehan et al. 2004; Carrascal et al. 2012a). On the other hand, sun radiation has both illumination and thermal benefits with important consequences on winter bird distribution at local scales (Shields and Grubb 1974; Stapanian et al. 1999; Huertas and Díaz 2001; Carrascal and Díaz 2006). Diurnal birds need a minimum light intensity for foraging, and the length of direct sun incidence is the ultimate determinant of the available time for foraging each day. Moreover, received heat from sun radiation has a pronounced effect in reducing thermoregulatory costs at low temperatures in temperate and boreal latitudes (De Jong 1976; Lustick et al. 1978; Carrascal et al. 2001). Finally, direct sun radiation on clear days favors the activity of prey such as ectothermic arthropods, increasing food availability for birds (Honek 1997; Carrascal et al. 2001). Therefore, it is expected that small diurnal passerines will select sunlit areas (with high exposure to sunlight) in order to reduce the inactive nighttime period and to increase the accumulated benefits derived from solar radiation.

Vegetation structure also plays a prominent role in defining the space that provides roosting opportunities and feeding substrates for bird populations (Cody 1985; Wiens 1989). To survive winter conditions, birds must explore their environment in order to familiarize themselves with their habitat, tracking the changing food availability to reduce the risk of starvation (Naef-Daenzer 2000). Therefore, the previous knowledge of the area must also be of value for winter residency, considering social dominance and food storing behavior (Sandell and Smith 1991; Koivula et al. 1993; Brotons and Haftorn 1999; Broggi and Brotons 2001), so we expect that the pattern of winter roosting will somehow reflect the previous exploitation of the area (i.e., previous occupancy during the breeding season for sedentary species).

Winter is a hard period for birds living in montane oakwoods of continental cold Mediterranean climate (Senar and Borrás 2004), which need to find the most favorable forest patches in order to ameliorate the limiting conditions of winter weather. Here, we investigate factors associated with roost site selection, including both the environmental conditions at night and the foraging scenario just before and after roosting time. The specific goal is to test the predictions related to the influence of altitude, temperature, sun radiation, habitat structure, and the previous knowledge of the area summarized in Table 1. We study woodland passerines wintering in a montane Mediterranean forest of central Spain of cold continental climate within a heterogeneous forest according to habitat structure and topographic complexity that generates

Table 1. Predictions of bird preferences for night-roost sites and hypotheses related to predictions.

Predicted higher occupation of roost sites	Related hypotheses
At lower altitudes	Harsh weather probability
With higher nocturnal temperatures	Thermoregulation costs
With higher diurnal temperatures	Thermoregulation costs
With higher potential sun radiation	Thermoregulation costs
	Foraging period length
	Prey activation - food availability
With higher development of tree crown	Habitat preferences
With higher previous breeding occupancy	Previous knowledge of resources

a high variability in the hill-shading pattern We investigate the determinants of winter roost site selection by using nest boxes of identical characteristics, set on a regular basis throughout a study area that constitutes a combination of especially harsh environmental conditions depicting an energy-limiting winter scenario in which birds should use the habitat efficiently in order to minimize thermoregulation costs of winter residency.

Methods

Study area and period

The study was carried out in a monospecific oak forest (*Quercus pyrenaica*) located in the Guadarrama Mountains, central Spain (40º53'N-3º50'W). The study area covers 61 ha of a craggy and predominantly north-facing slope ranging between 1,250 and 1,600 masl, the altitudinal superior limit of oak forests in the region (Blanco et al. 1997). The high altitude along with the orientation imposes harsh conditions during the winter, with the least possible hours of sun radiation, and temperatures usually bellow 0 ºC. The area received a relatively low insolation during the winter study period (an average of 3 h and 21 min of sun per day, i.e., 36 % of light hours at winter solstice, with 36% of days with >5 h of sun per day; average data from Navacerrada Pass and Colmenar Viejo meteorological stations, from 23th November to 13th January; Spanish Agencia Estatal de Meteorología- Ministerio de Medio Ambiente, Medio Rural y Marino).

The study was conducted on 52 days around winter solstice (from 23th November 2010 to 13th January 2011), i.e., the most stringent period of the winter considering the relative duration of day and night (9:14 h - 14:46 h, respectively, at winter solstice). The study area has 159 wooden nest boxes installed in 2008 in a grid at a regular distance of c. 50 m between adjacent boxes (c. a density of 2.6 nest boxes per hectare; Fig. 1). These nest boxes have been used as regular breeding sites since 2008 by the pied flycatcher (*Ficedula hypoleuca*; transaharian migrant) and the following three resident species: blue tit (*Cyanistes caeruleus*), great tit (*Parus major*) and nuthatch (*Sitta europaea*). In a pilot survey outside the study period of 52 days, we observed that nest boxes were only used as winter roost sites by blue tits, great tits, and nuthatches and that each nest box was only used each night by one individual (i.e., communal roosting was never observed). We used wooden nest boxes (base 11 × 13 cm, height 20 cm, 15 mm thickness of walls, centered entrance of 30 mm diameter), with a plastic pipe of 9 cm long installed in the entrance to avoid predation by Mustelidae, the garden dormouse (*Eliomys quercinus*) and the great spotted woodpecker (*Dendrocopos major*). Nest boxes were hanged from branches with a metal hook at an average height of 3.76 m (0.49 SD). The occupation of nest boxes may

be favored by the scarcity of natural cavities in this managed forest (Camprodon et al. 2008). Occupation of nest boxes by blue tit, great tit, and nuthatch was registered during the preceding breeding season (spring 2010; data obtained by OG in the context of other research program).

Two habitat measurements of 10 m around each nest box were obtained as follows: average oak height and number of oaks larger than 10 cm of trunk diameter at breast height. These habitat variables define tree crown characteristics and were obtained considering the habitat preferences of the studied species (Perrins 1998) and winter habitat use in the study region (Carrascal et al. 1987).

Air temperatures

To measure winter air temperature, we set 10 temperature data loggers (Onset HOBO® Pendant, model UA-002-64, resolution 0.1 ºC) covering the whole spatial variability in altitude, cardinal orientation, and location (in the latitude-longitude plane) within the study area. In average, there was one logger in a circle of 126 m radius. Loggers were placed on thick oak trunks, oriented to the north and at approximately 1.5 m above ground, in such a manner that they never received direct solar radiation (i.e., air temperature was measured in the shade). Data loggers recorded air temperature every 10 min minutes from 1st December 2010 to 13th January 2011. For each recording day (144 measurements), we calculated average daytime temperature, average night temperature, maximum daytime temperature, and minimum night temperature. Temperatures for these 44 winter days were averaged for each sampling point. In order to avoid multicollinearity in data analyses and considering that these four temperature measurements were highly correlated across days and sampling points, we selected the two least correlated measurements as follows: minimum night and average daytime temperature. These two temperatures have a different functional meaning that is related to maximum thermoregulatory costs at night and average thermoregulatory costs at daytime, respectively.

To estimate the minimum night and average daytime temperature in the location of each of the 159 nest boxes, we used a weighted-averaging approach considering the temperatures registered in the 10 points where the temperature loggers were placed. The temperature for each nest box location was calculated considering the temperatures registered by all loggers located in a radius of 350 m, weighted by the inverse of their distances (this threshold leads to an average of 3.3 temperature loggers used for each nest box, which we considered appropriated for this scenario). This methodological approach is similar to the interpolation of weather variables into pixelated maps using the available small number of meteorological stations.

Sun radiation at nest boxes

Potentially received sun radiation at each nest box location was obtained using ArcMap® (v10) together with a digital elevation model of the terrain (30-m resolution ASTER Global Digital Elevation Model). Sun illumination raster layers accounting for sun position, terrain slope, cardinal orientation, and hill-shading effect were generated for the study area at the winter solstice, every 15 min of daytime (with values ranging from 0 to 254, where 0 is complete lack of sun radiation and 254 is perpendicular to solar radiation). Hill-shade figures were converted to incident solar radiation per area (KW/m^2). Required azimuth and sun elevation angles were obtained from a web application at http://www.sunearthtools.com, while incoming direct solar radiation was obtained from the Radiation On Collector Program (http://www.builditsolar.com). Based on these 15-min values, we calculated the duration of sun incidence at each nest box and an index of cumulative sun radiation during the whole day at winter solstice (kilojoules per square meter). These two measures were highly correlated in the study

area (r = 0.86, n = 159). In order to avoid redundancy, in the analyses, we only considered the index of sun radiation, which is probably more informative. This index corresponds to the maximum amount of radiation potentially received at each site under anticyclonic sunny conditions. The influence of cloud cover related to regional meteorological conditions was homogeneous throughout our relatively small study area, and therefore, potential sun radiation is a good index of relative differences among nest boxes.

Winter nest box occupation

Nest boxes were carefully cleaned of feces at the end of the previous spring and at the beginning of the study (23-24th November) in order to set homogeneous initial conditions for all nest boxes in terms of parasitism infestation or predators traces (Christe et al. 1994; Ekner and Tryjanowski 2008). We put standard-sized filter paper (11 × 13 cm) covering the base of the nest boxes to facilitate the detection of feces. The presence of feces in nest boxes was checked only once, at the end of the study (12th/13th of January 2011). Nest boxes were only manipulated during daylight hours (2 h after sunrise and 1 h before sunset) to avoid disturbance and undesirable influence on occupation decisions (Tyller et al. 2012). We found no birds during the daytime in any of the 159 nest boxes revised both at the beginning and at the end of the study and we, consequently, assume that birds usually did not occupy nest boxes during daytime. Therefore, the presence of feces in nest boxes can be assumed as a reliable indicator of nocturnal occupation (Dhondt et al. 2012). Winter nest box occupation at night was defined by the presence of feces throughout the 52 days of study (from 23th/24th of November 2010 to 12th/13th of January 2011).

Data analyses

The comparison between occupied and unoccupied nest boxes was carried out by Monte Carlo analyses (Davison and Hinkley 2007). First, we obtained the *t* test statistics comparing the averages of occupied (n = 38) and unoccupied (n = 121) nest boxes, considering the seven original variables (altitude, potential sun radiation, average minimum night temperature and average diurnal temperature during the whole study period, average oak height and density 10 m around each nest box, and the occupation of nest boxes in the preceding breeding season of April-June 2010). Second, a randomization process was carried out maintaining the data in each row (i.e., the values of the seven predictor variables within each nest box location and the true associations between them), obtaining a bootstrap sample of 159 nest boxes, and defining a first group of null-occupied (n = 38) and null-unoccupied (n = 121) nest boxes. The aim of this randomization procedure was to preserve the spatial structure of the data, accounting for the spatial autocorrelation of the data and for the possible pseudoreplication derived from the fact that the same individual bird may occupy more than one nest box on different nights. Third, seven *t* tests were carried out considering the null groups of occupied and unoccupied nest boxes, thus obtaining a null *t* statistic for the seven original variables. This process was repeated 9,999 times. Fourth, the actual figures of the *t* statistic testing occupied *vs.* unoccupied nest boxes were compared with 9,999 null *t* values obtained for each one of the seven predictors analyzed. Significance of *t* tests comparing the actual averages of occupied and unoccupied nest boxes was estimated considering the position of these true *t* statistics within the null distribution of *t* figures by means of the percentiles using a one-tailed approach according to predictions in Table 1. Analyses were carried out using the Resampling and Monte Carlo functions of "Pop Tools 3.0" (http://www.cse.csiro.au/poptools/) within Microsoft Excel 2010.

A principal components analysis (PCA) with a Quartimax rotation was carried out with the seven variables describing the 159 nest boxes to obtain a reduced number of factors that summarized the relationships

among variables and defined environmental gradients within the study area. Four factors with eigenvalues larger than one were retained. The principal components analysis was carried out using STATISTICA 10.0 (StatSoft Inc., Tulsa, OK, USA). Using the factor scores of each nest box (i.e., position of each nest box in the principal components), the preceding testing approach based upon Monte Carlo analysis was repeated, on this occasion testing for the differences between the average position of occupied and unoccupied nest boxes in the four environmental gradients. Two-tailed *p*'s were estimated because it was not possible to make *a priori* predictions about the structure of the relationships among variables in the principal components. Finally, a spatial eigenvector mapping analysis (SEVM) was carried out to account for spatial autocorrelation in nest box occupancy (Diniz-Filho and Bini 2005; Dorman et al. 2007). SEVM is based on the idea that spatial arrangement of sample locations can be translated into explanatory variables that capture spatial effects. Nest box occupancy was treated as a binomial variable and the four principal components obtained from the PCA as continuous predictors. The eigenfunction decomposition of the spatial connectivity matrix among the 159 nest boxes yield seven spatial autocorrelation filters that reduced spatial autocorrelation in the residuals of the model (nonsignificant according to Moran's I). SEVM was carried out using SAM package (Rangel et al. 2010).

Results

There was a very broad variation in environmental variables among nest box locations (range: min–max); potential cumulative sun radiation: 15–3,604 kJ/m^2 (on winter solstice), altitude: 1,281–1,599 m, average minimum night temperature (from 1st December to 13th January): -0.60 to -0.01 ºC, average diurnal temperature (from 1st December to 13th January): +3.80 to +4.90 ºC, oak height: 4–15 m, oak density: 6–127 oaks per 314 m^2. Only 38 of a total of 159 available nest boxes were occupied for winter roosting (24%). Most nest boxes chosen by birds for winter roosting were not occupied the previous breeding season (81%), and only 12% of nest boxes used for breeding were later used for winter roosting (Fig. 1).

According to predictions derived from the hypotheses explaining winter preferences for roost sites (Table 1), characteristics of woodland locations with occupied nest boxes significantly differed from those with unoccupied nest boxes in only the amount of potential sun radiation and average oak height (Table 2). Birds preferred woodland locations with higher potential sun radiation and taller oaks around nest boxes. Nest box occupancy in the preceding breeding season did not show the predicted effect: wintering birds preferentially roosted in nest boxes not used during the previous breeding season. Altitude and temperatures did not show the predicted effects: occupied roost sites were 52 m higher, had nearly identical minimum night temperatures, and were 0.13 ºC colder during the day than unoccupied nest boxes (one-tailed *p*'s > 0.85). Oak density around the nest boxes did not influence their occupancy. Therefore, selection of woodland locations to spend the night under identical controlled situations (i.e., roosting within the same wooden nest boxes), was only dependent on subtle variations in sun incidence related to topography and maturity of the oaks.

The principal component analysis (PCA) provides four factors with eigenvalues higher than one, which accounted for 80.1% of original variance (Table 3). The first component accounts for one-third of original variance, defining a natural gradient of increase in potential sun radiation with increasing altitude and decreasing diurnal temperature and nest box occupancy the previous breeding season. The second (16%), third (16 %), and fourth (15 %) components order the nest boxes according to average tree height, oak density, and minimum night temperature, respectively. Thus, a large

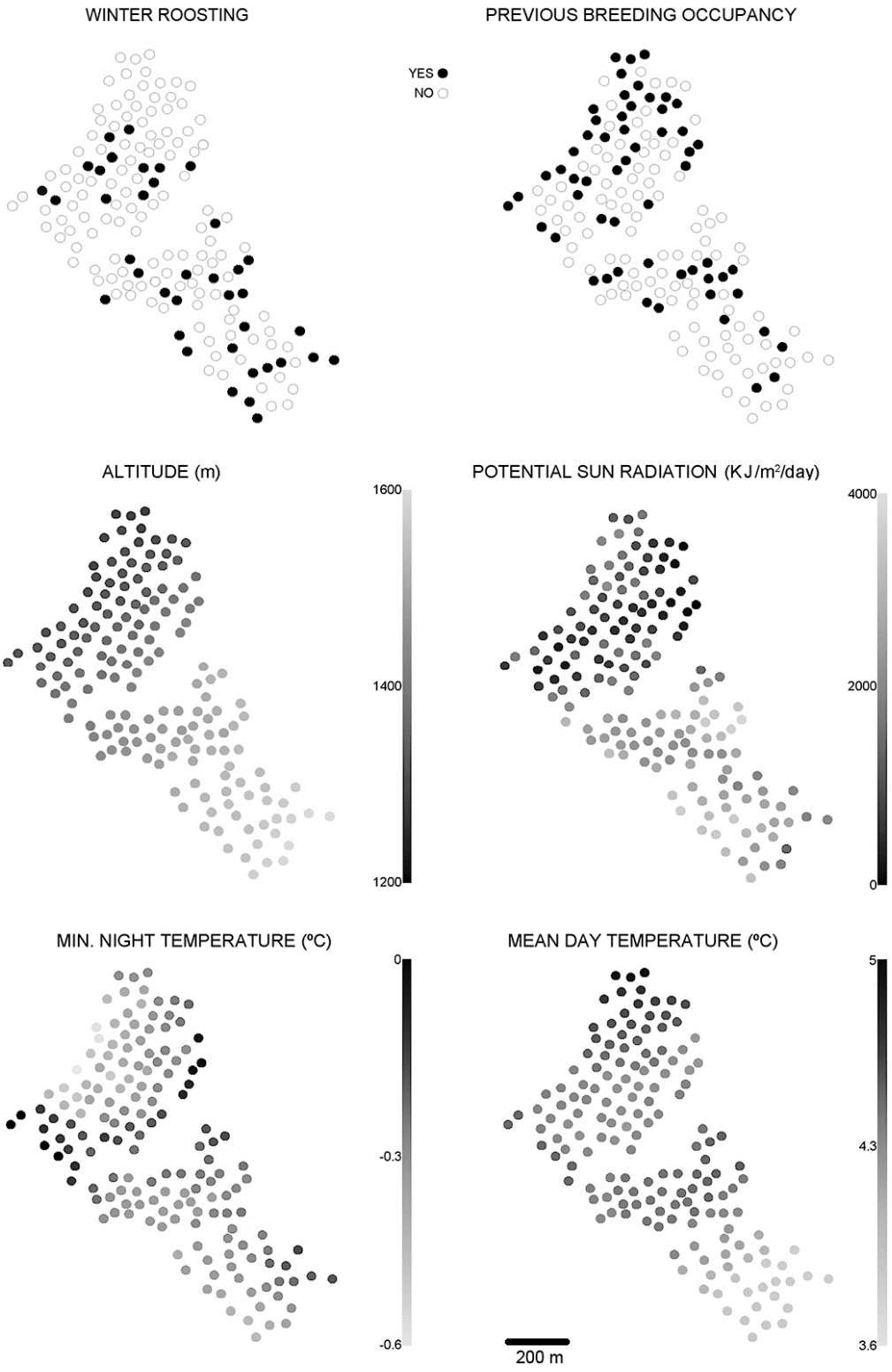

Figure 1. Location of 159 nest boxes in the study area, and the spatial variation of night occupancy of nest boxes throughout 52 days around the winter solstice (WINTER ROOSTING) and five predictor variables used in the analysis shown in Table 2.

Table 2. Mean and standard deviation (SD) of seven variables describing the characteristics of occupied (OCCUP, n=38) and unoccupied (UNOCCUP, n=121) nest boxes for winter roosting. Statistical significance of the differences between means were obtained using *t*-tests and Monte Carlo analysis building null distributions of *t* statistics (9,999 randomization trials; see Data analyses for more details). Significance tests are one-tailed according to predictions in Table 1. Potential sun radiation is the cumulative radiation obtained in an anticyclonic sunny day in winter solstice.

	OCCUP		**UNOCCUP**			
	Mean	SD	Mean	SD	Prediction	One-tailed *p*
Altitude (m)	1,471.9	91.3	1,419.6	89.5	Lower	0.999
Minimum night temperature (ºC)	-0.31	0.09	-0.29	0.12	Higher	0.856
Average day temperature (ºC)	4.21	0.23	4.35	0.21	Higher	0.999
Potential sun radiation (KJ/m^2)	1,953.0	902.4	1,557.0	864.7	Higher	0.010
Oak height (m)	10.1	1.8	9.2	2.0	Higher	0.005
Oak density (#/314 m^2)	50.5	27.4	53.1	27.5	Higher	0.684
Previous breeding occupancy (%)	18.4	39.3	41.3	49.4	Higher	0.997

amount of variation in oak height and density was not related to altitude, temperatures, or potential sun radiation in our study area, as they entered in different orthogonal components. Average position of occupied and unoccupied nest boxes significantly differed in the first two components. Occupied nest boxes during winter received more sun radiation, were located at higher altitudes with lower average diurnal temperatures, and were less occupied for reproduction the previous breeding season, than unoccupied nest boxes. On the other hand, occupied nest boxes for winter roosting were surrounded by taller oaks than unoccupied ones. Nearly identical results were obtained using SEVM analysis as follows: only the first and second components of the PCA were positively and significantly related to nest box occupancy after accounting for spatial autocorrelation.

Discussion

To our knowledge, this is the first study relating sun radiation during daytime to winter night roosting preferences. The prominent influence of sun radiation just before and after the critical night-fasting period probably precluded the manifestation of other classical effects such as temperature or altitude. Wintering birds identified the fine-grained mosaic of radiation generated by the hill-shade effect and chose to roost at forest patches with higher sun radiation.

The great importance of sun radiation for wintering birds may respond to three complementary causes. First, a terrain with a longer sun incidence has greater illumination levels, even when the sky is cloudy, extending the time available for foraging. If small birds are strongly pressed to feed in order to cope with winter requirements because of their high metabolism relative to their small body masses, the low food availability, low temperatures, and the long fasting night period (e.g., Gibb 1954), they should prefer those woodland areas with longer day lengths and better foraging conditions (amount of sun radiation and duration of sun incidence were highly correlated: r = 0.86; see also Carrascal et al 2012b for the importance of day length on tit abundance along a latitudinal gradient). Second, birds may benefit from the heating effect of sun radiation on cloudless days, accounting for a 10-15 ºC increase in operative temperature under winter windless

Table 3. Principal components analysis performed with seven variables defining environmental characteristics in 159 locations with nest boxes (factors PC1-PC4). In bold type are factor loadings > 0.5. Mean and standard deviation (SD) of factor scores of occupied (n=38) and unoccupied (n=121) nest boxes in each principal component. Statistical significance of the differences between means were obtained using *t* tests and Monte Carlo analysis building null distributions of *t* statistics (9,999 randomization trials; see "Data analyses" for more details). Results of the spatial eigenvector mapping (SEVM) show the partial coefficients and significance of principal components after considering seven spatial autocorrelation filters.

	PC1	PC2	PC3	PC4
Altitude	**0.92**	-0.03	-0.13	0.10
Minimum night temperature	0.03	-0.05	-0.01	**0.97**
Average day temperature	**-0.70**	-0.36	0.35	-0.09
Potential sun radiation	**0.79**	-0.32	0.04	-0.25
Oak height	0.00	**0.91**	0.06	-0.06
Oak density	-0.25	0.00	**0.85**	-0.04
Previous breeding occupancy	**-0.53**	-0.27	-0.48	-0.15
Eigenvalue	2.32	1.14	1.10	1.05
% variance accounted for	0.33	0.16	0.16	0.15
Factor scores of occupied nest boxes				
Mean	0.51	0.36	0.06	-0.15
SD	0.95	0.96	0.97	0.86
Factor scores of unoccupied nest boxes				
Mean	-0.16	-0.11	-0.02	0.05
SD	0.97	0.99	1.01	1.04
t test (two-tailed *p*)	0.0006	0.011	0.697	0.267
Coefficients of SEVM	0.239	0.077	-0.007	-0.038
Significance	<0.001	0.011	0.829	0.224

conditions (see Carrascal et al. 2001 and Carrascal et al. 2012a for the same woodlands in Guadarrama mountains). Several laboratory studies have shown the significant effect of sun radiation on passerines, dropping the lower threshold of temperature tolerance and reducing the metabolic costs of thermoregulation (Lustick et al. 1970; 1978; De Jong 1976; Wood and Lustick 1989; Wolf et al. 2000). Finally, sun radiation indirectly enhances foraging efficiency of birds by increasing the activity of ectothermic arthropods (Avery and Krebs 1984; Honek 1997; Carrascal et al. 2001).

Contrary to our prediction, wintering birds did not show any preference for roosting at lower altitudes (Tables 2 and 3). Due to orographic effects in our study area, the patches located at higher altitudes turned out to be those with a higher sun incidence (Table 3, Figure 1). This counterintuitive preference for high elevations due to increased sunshine was also shown in black-and-white snub-nosed monkeys wintering in the Trans-Himalayans (Quan et al. 2011).

Yet surprisingly, selection of roost sites was not influenced by environmental temperature, either nocturnal or diurnal (Table 2). Our results are in accordance with Thiel et al. (2007), who reported that microclimate does not influence selection of night roosts by the capercaillie in central

Europe. Thermal properties of cavities for roosting may buffer environmental variation in outdoor night temperature (Paclik and Weidinger 2007; Coombs et al. 2010; Grüebler et al. 2013). This fact may reduce the importance of temperature in the selection of night roosts, allowing other factors such as habitat or resources surrounding the roost site to gain importance. Moreover, Polo and Carrascal (2008) demonstrated that temperature *per se* does not influence night body mass loss in a small passerine, the coal tit (*Periparus ater*), in the same region. Nocturnal body mass loss mainly depended on the level of body mass at dusk and daily body mass gain in the previous day, supporting the influence of proximate effects related to the regulation of body reserves the preceding day, instead of the expected pure physiological energetic balance (i.e., lower temperature related to higher resting metabolism; Calder and King 1974; Carey 1996).

The preference for woodland patches with taller oaks is consistent with the preference of the studied species for mature oakwoods, considering they are tree canopy gleaners and trunk foragers (Perrins 1998; see Carrascal and Díaz 2006; Carrascal et al. 2012c for the study region). Overlapping this general pattern of habitat preferences with the selection of locations where cumulative solar radiation is greater, a practical recommendation may be derived from our results as follows: forest management practices should preserve the most mature forests considering their location on those slopes more exposed to solar radiation during winter, in order to enhance habitat suitability for woodland birds in these Mediterranean deciduous forests of continental cold climate.

Finally, the decoupling between occupancy of nest boxes in winter and the previous breeding season may reflect how birds adjust their distribution to the specific requirements of the season, imposed by both the environment and the phase of their life cycle. In spring, birds may avoid higher altitudes with more weather instability, where a sudden cold spell can drastically compromise parental investment (Sanz and Moreno 1995; Seoane et al. 2013).

The applicability of the habitat use pattern described in this paper cannot be generalized to every environmental condition or geographical location. Geographic and orographic variation in winter sun incidence defines the background where the phenomenon may be ecologically relevant for these species. For example, cloudiness and day length vary from less than 50 % of the 9–10 h of winter daylight in southern Europe to more than 70 % of less than 5 h of daylight at latitudes above 55º (Henderson-Sellers 1986). Thus, possibilities for minimizing costs of thermoregulation by selecting sunlit patches are scarce at higher latitudes with few clear days available in winter. Moreover, this behavior can only operate in mountainous areas where the hill-shade effect introduces a large variation in sun radiation at small spatial scales. For example, in the study area, the potential sun radiation received at different nest box locations varied enormously both in length (from 15 min to 7 h) and in magnitude (from 15 to 3,604 kJ/m^2 in the winter solstice day; Fig. 1). Therefore, selection of roost sites according to differential solar radiation received by a forest patch could play an important role at mountainous areas of cold climate with frequent anticyclonic conditions.

Aknowledgements

This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Educación y Ciencia. Óscar Gordo was supported by a Juan de la Cierva grant (JCI-2009-05274). The authors thank the Natural Park of Peñalara for the authorizations to access the study area. We also thank Vicente Polo, Jesús Rodríguez and Carlos Lusa for their help with field work, Teresa Cuartero for GIS assessment, and Claire Jasinski for improving the English of the manuscript.

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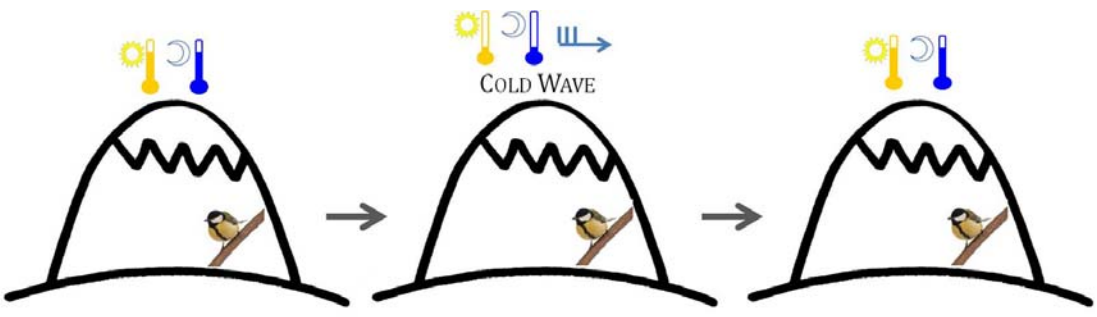
Chapter 3

Woodland Mediterranean birds can resist an extreme cold wave


COLD WAVE

Las aves forestales mediterráneas pueden resistir una ola de frío extrema

Objetivo Analizar la resistencia de tres especies de paseriformes invernantes, del gremio de los forrajeadores arbóreos, a una ola de frío extrema.

Localización Robledal montano mediterráneo de la Sierra de Guadarrama (escala de paisaje).

Métodos Monitoreamos la temperatura, el viento y la abundancia relativa de *Parus major*, *Cyanistes caeruleus* y *Parus cristatus* en 15 puntos de muestreo a lo largo de tres periodos: antes, durante y después de la ola de frio que sacudió Europa en febrero de 2012.

Resultados y discusión Nuestros resultados descartan que la ola de frío provocara una mortandad generalizada o una migración temporal de las poblaciones de estudio. La abundancia de estas especies no disminuyó con ola de frío. Sólo *P. cristatus* se desplazó a las zonas más protegidas del viento para minimizar su efecto negativo.

Conclusiones Estas tres especies de aves forestales fueron capaces de soportar una ola de frío seca que fue estadísticamente extrema en términos de temperatura y sensación térmica, de acuerdo con los registros climáticos históricos de la región. Parece que, al menos mientras que los sustratos de forrajeo no se encuentren cubiertos por la nieve o el hielo, las aves mediterráneas son capaces de resistir una caída excepcionalmente drástica de las temperaturas.

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Villén-Pérez S, Carrascal LM. Woodland Mediterranean birds can resist an extreme cold wave

Woodland Mediterranean birds can resist an extreme cold wave

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Abstract The ecological consequences of climate extreme events are still poorly understood, especially those related with cold episodes. Winter cold spells might imperil the energy balance of small passerines, thus compromising their survivorship. Here we analyze how the abundance and habitat use of three tree-gleaning passerine species wintering in a montane oakwood of central Spain at ca. 1300 m a.s.l. was influenced by the cold wave that hit Europe in February 2012. We monitored temperature, wind and the relative abundance of *Parus major, Cyanistes caeruleus* and *Parus cristatus* in 15 plots throughout three periods: before, during and after the cold wave. Our results clearly discard widespread mortality and temporal migration of the studied passerine populations. The abundance of these species did not diminish during the cold wave, and only the long-tailed tit moved to the less windy woodland plots, probably to mitigate the deleterious effects of wind chill. Therefore, these forest birds were able to cope with a dry cold wave that was statistically extreme in terms of temperature and wind chill, according to the historic climate records of the region. It seems that, at least when foraging substrates are not heavily covered by snow or ice, woodland Mediterranean birds can resist an extreme cold wave.

Keywords: *Cold wave · Harsh weather · Mediterranean oakwoods · Temperature · Tree-gleaning birds · Wind chill*

Introduction

Assessing the ecological effects of extreme climate events poses a major challenge because of the nature of such events: they are short, rare, low predictable, and highly dependent on the context. The extremeness of a climatic event have to be defined based on the historic climate record, because the ecological response of species may depend on what the population have experienced in the past (Jentsch 2006, Jentsch et al. 2007, Gutschick et al. 2010, Smith 2011a,b). The ecological responses to statistically extreme climatic conditions have been approached through both experiments and opportunistic observational studies. A number of experiments show a surprising lack of strong ecological responses (Smith 2011a and references therein), but sadly negative results are less often reported in observational studies (but see Jiguet et al. 2011). This may reflect a biased motivation for episodes with obvious ecological responses (e.g., widespread mortality of a species; Smith 2011a) or difficulties publishing negative results (Fanelli 2012). However, this research discipline may benefit from combining the results obtained from both extreme events and "normal" natural situations to disentangle the triggers of the responses in each system.

Ecological responses to climate extremes may range from temporal migration of individuals, to population crashes, to long-term changes in community structure or ecosystem function (see reviews of Jiguet et al. 2011 and Smith 2011b, and references therein). In a global warming scenario, the emphasis is rarely put on extreme cold events

(e.g., Jentsch and Beierkuhnlein 2008, Cattiaux et al. 2013). Nevertheless, severe weather might imperil the energy balance of wintering small passerines beyond normal thresholds. At temperate latitudes, birds have to cope with winter temperatures well below their thermoneutral zone (Calder and King 1974, Kendeigh et al. 1977), and their metabolic costs of thermoregulation increase with decreasing temperatures and increasing wind speeds (eg. Wolf and Walsberg 1996). Accordingly, these species select the warmest areas at a landscape scale to overwinter, where the thermoregulation costs are minimized (e.g., Canterbury 2002, Meehan et al. 2004, Evans et al. 2006, La Sorte et al. 2009, Carrascal et al., 2001, 2012).

Here we analyze the resistance to change of the abundance and local distribution of three resident woodland passerines facing a cold wave that hit Europe in February 2012. The studied species belong to a tree-gleaning guild wintering in montane areas of the Iberian Peninsula. We postulate three possible mechanistic scenarios of response to this extreme cold wave (Figure 1), that would work over the steadily increase in population abundance usually registered in these forests from the winter solstice to the beginning of the following breeding season (O Gordo, JJ Sanz and J Potti, com pers). First, the cold wave may have not negatively influence species local abundance, because they have local adaptations to cope with severe weather (e.g., changes in foraging behavior and habitat use). In this case, the natural steady increase in abundance should be maintained or only slowed down during the cold wave. Second, the cold wave should impose a temporal migration of part or the whole wintering populations, which would return after the end of the cold wave to their winter territories and restore normal abundance levels. And third, the cold wave could provoke widespread population mortality, so local abundance would decrease during the cold wave but would not recover after it reaching previous levels. To test these hypotheses, we monitored local abundance of birds before, during and after the cold wave, measuring the local environmental conditions in terms of temperature, wind speed and wind chill. We also analyzed the environmental determinants of the spatial variation in abundance within the study area, to detect if individuals staying during the cold wave would move to the warmer and less windy forest patches to mitigate the deleterious effects of wind chill.

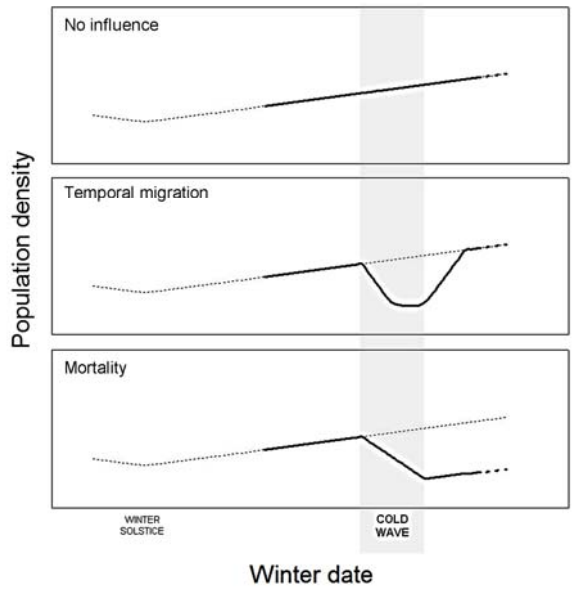

Figure 1. Three possible mechanistic scenarios of response of bird populations to the studied cold wave (grey area). All are postulated to work over the background steady increase in population abundance usually registered in these forests from the winter solstice to the end of the winter season (thin dashed line). Postulated tendencies over the study period (thick solid line) and tendencies until the end of February (thick dashed line) are highlighted. The cold wave could not influence species abundance at all, promote a temporal migration of individuals, or provoke a widespread mortality of the population.

Methods

Study area and species

Field work was conducted in an oakwood located in Navacerrada (40.725ºN, 4.033ºW; Sierra de Guadarrama, Central Spain). The study area is a mosaic of open and dense patches of a monospecific forest of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), mainly dominated by young trees

of 6-14 m. Altitude ranges between 1200 and 1360 m a.s.l. The climate is continental cold Mediterranean, with dry and hot summers and abundant snowfall and frost in winter. For more details on the vegetation structure and bird communities of these forests in Central Spain see Seoane et al. (2013).

The focal species were those belonging to the tree-gleaning guild of the mountainous oakwoods of Central Spain (Carrascal *et al.* 1996): *Parus major* (great tit), *Cyanistes caeruleus* (blue tit) and Aegithalos caudatus (long-tailed tit). They are residents and relatively abundant birds throughout the winter in the oak forests of the Guadarrama mountains (Carrascal and Díaz 2006; Seoane et al., 2013). These small-sized species mainly forage in the twigs and small branches of trees, although they can also use the forest floor for foraging (especially the great tit). The study was centered in these species because passerines foraging in small branches are more severely affected by low temperatures and high wind speed (Grubb 1975). Moreover, they do not store food, so they rely only in body reserves to overcome severe periods of inclement weather (Perrins, 1979). The increase in population abundance of these species during the cold wave due to the arrival of temporal migrants from higher altitudes is discarded because the study area is an insular oakwood surrounded by pinewoods not inhabited by these species (or very scarce in the case of the great tit). Other small tree-gleaning species were present in the study area, but were very scarce so as to obtain a large and representative sample to measure abundance changes among study periods of different weather (lesser spotted woodpecker, *Dendrocopos minor*, nuthatch, *Sitta europaea*, short-toed treecreeper, *Certhia brachydactyla*).

Three study periods were defined: mild-weather period prior to the cold wave (hereafter Before CW; sampled on 3, 9, 10, 11 January 2012), cold wave (CW; 2, 3, 4, 8 February 2012), and mild-weather period after the cold wave (After CW; 17, 18, 22, 23, 24 February 2012).

Statistical characterization of the cold wave in February 2012

The meteorological characteristics of the cold wave studied here were compared with the daily historical record from the period 1946-2012 (data from the nearby meteorological station in Navacerrada Pass, located at 7 km from the study area, 1894m, AEMET; n = 24193 days for temperature data; n = 18843 days for wind data). Cold days were defined as those with minimum temperatures below the long-term 5th percentile of daily minimum temperatures, or wind chill temperatures below the long-term 5th percentile of daily wind chill temperatures (analogous to Della-Marta et al. 2007 criterion to define hot days).

The month of February 2012 was the coldest February in Spain since 1956 (i.e., the one with the lowest daily averages of minimum temperatures in 56 years). We focus on a cold wave of 12 days, within which there was three "sub-waves" of three consecutive cold days each (with daily minimum temperatures below the long-term 5th percentile of daily minimum temperatures). Three cold days in a raw cannot be considered a statistically extreme event in the study area (where the upper 5th percentile of number of consecutive cold days is five). However, temperatures were very low during the whole cold wave and, during this 12 days-period, the mean of the minimum (-11.6 ºC at Navacerrada Pass, 1894 m asl), average (-8.3 ºC), and maximum (-5 ºC) temperatures were all within the lower 5th percentile of historical records (-8 ºC, -10 ºC and -5 ºC, respectively).

During the 12 days, average wind speed was 4.9 m/s (data for 10 days with wind records), which is above the upper quartile of historically-recorded average wind speeds (4.7 m/s). The extreme low temperatures coupled with these relatively strong winds resulted in an average wind chill temperature (WCT; following Osczevski and Bluestein 2005) of -15.3 ºC, which is well below the lower historical 5th percentile (-

11.7 ºC). During the cold wave there was at least four cold days in a raw considering the WCT (days with WCT below the lower historical 5th percentile). Four cold days considering WCT is a statistical extreme event in the study area (where the upper 5th percentile of number of consecutive cold days is four). In addition, we sampled during the windiest days of the cold wave, with an average wind speed of 6.4 m/s and an average WCT of -19.7 ºC. The cold wave in the area was not accompanied by strong precipitations (average of 5 mm for the 12 days; 1.5 mm for sampling days).

Bird censuses, habitat structure and temperature and wind measurements

We measured local bird abundance using point count stations lasting 5 min, recording all birds heard or seen within 25 m radius (0.19 ha). The census began arriving to the center of each plot, and continued following the same protocol in all samples: we walked very slowly within the area of the census plot over an imaginary circumference of radius 12.5 m. By means of this approach we pursued to maximize the detection probability of the birds within the census plot even under windy or snowy circumstances. Thus, our census method does not intend to measure exact bird densities (i.e., birds / ha), but to obtain a measure of habitat use in 15 different woodland plots under different weather conditions. After the census, we walk at a brisk path in order to reach the following sampling point as soon as possible in order to minimize the probability of sampling the same birds in two consecutive plots (i.e., we moved faster than the study species usually do while moving in the forest). The two authors carried out the censuses. Five teen woodland plots of 25 m radius were established within the study area. Plots were separated by at least 250 m.

We followed an *a priori* planned protocol of sequential sampling in order to obtain a completely overlapped distribution of the time of the day when the 15 plots were sampled. To accomplish this goal, we began each sampling day with a different sequence of contiguous plots (e.g., 1, 2, … 14, 15; 5, 6, … 15, 1, … 4; etc). Sampling began at 9:00 h and ended at 17:00 h GMT.

A 25-m-radius plot was placed within each census point to sample two vegetation structure variables related to maturity and density of the oakwood plot: average height of trees and number of trunks with a diameter larger than 10 cm at the breast level. Average oak height was 10.2 m (range: 6-14; sd = 2.7) while average oak density was 146 trees / 0.19 ha (range: 62-303; sd = 68.9). All vegetation structure measurements were obtained by the same person within the same sampling day (LMC).

To describe local fine-grained variation in winter air temperatures, one temperature logger (Onset HOBO Pendant, accuracy 0.47 ºC) was set in each oakwood plot. Loggers were placed on trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every 5 min from 01 January to 28 February 2012. Thus, we could link the moment of the census of each woodland plot to the prevailing temperature while sampling (using the nearest temperature record to the time when the census began). Wind speed during the census was measured as the average of two wind measurements obtained with a portable handheld meter during 30 seconds (Ventix Thermo-Anemometer 8908); one 30 seconds before the beginning of the census, and another immediately after the end of the 5 min census. For each 30-sec sampling period we obtained the maximum registered wind speed.

Data analyses

To test the hypotheses in Figure 1, local abundance of birds before the cold wave (B-CW), during the cold wave (CW) and after it (A-CW) were compared using t-tests. The comparison was carried out by Monte Carlo analyses (Davison and Hinkley 2007). First, we obtained the *t*-test statistics for each species comparing the averages of the 15

woodland plots in B-CW vs. CW, and in CW vs. A-CW. Second, a randomization process was carried out maintaining the data within each plot (i.e., the values of the average number of birds recorded in [B-CW / CW] and [CW / A-CW]). The aim of this randomization procedure was to preserve the spatial structure of the data, accounting for the spatial autocorrelation of the data and for the possible pseudoreplication derived from the fact that the same individual bird may be present in more than one woodland plot on different days. Third, the *t*-tests were carried out considering the randomized data for each species in the B-CW vs. CW, and CW vs. A-CW comparisons, thus obtaining a null *t* statistic; this process was repeated 9,999 times. And fourth, the actual figures of the *t* statistic testing B-CW vs. CW, and CW vs. A-CW were compared with 9,999 null *t* values obtained. Significance of *t*-tests was estimated considering the position of these true *t* statistics within the null distribution of *t* figures, by means of the percentiles using a two-tailed approach.

We also analyzed the environmental determinants of the spatial variation in abundance within the study area during the cold wave to detect if individuals move to the warmer and less windy forest patches to mitigate the deleterious effects of the cold wave. The influence of temperature and maximum wind speed on bird habitat use during the cold weather period was analyzed by means of multiple regression, using the average number of birds per woodland plot as the response variable, and the temperature and wind speed as predictors. In order to control for the variation in habitat structure among the 15 woodland plots, the average height of oaks and oak density were also include as predictors. A multiple regression was carried out with the data for each species separately, obtaining the partial regression coefficients for temperature and wind speed. The significance of these coefficients was estimated by means Monte Carlo analyses. A randomization process was carried out bootstrapping the data on bird abundance for each plot. With the bootstrapped data, the same multiple regression analyses (one per species) were carried out, obtaining null partial regression coefficients; this process was repeated 9,999 times. The actual figures of the partial regression coefficients were compared with the 9,999 null values obtained. Significance of partial regression coefficients were estimated considering the position of the true coefficients within the null distribution by means of the percentiles using a two-tailed approach. As we were only interested in temperature and wind effects, the significance of partial regression coefficients for oak height and density were not estimated (and are not reported in the Results section). Analyses were carried out using the Resampling and Monte Carlo functions of «Pop Tools 3.0» (http://www.cse.csiro.au/poptools/) within MicroSoft-Excel 2010.

Results

Temperature and wind at sampling plots

Temperature measured locally during sampling at the 15 woodland plots fell an average of 12.9 ºC (from 9.1 ºC to -3.8 ºC) from the previous mild-weather to the cold wave period (Figure 2). After the cold wave it raised 14.2 ºC to reach an average of 10.4 ºC. Wind speeds increased an average of 4.21 m s^{-1} (from 0.83 m s^{-1} to 5.04 m s^{-1}) from the previous mild-weather period to the cold wave period, and decreased a similar amount after the cold wave to an average of 1.13 m s^{-1} (Figure 3).

The cold wave reduced the spatial variation in the average temperatures among woodland plots, from a range of 5.6 ºC in the previous mild-weather sampling period to 2.7 ºC during the cold wave (i.e., difference between the warmest and the coldest plots). Nevertheless, the variation in average wind speed among plots was higher during the cold wave (the range between the windiest and the least windy plot increased from 0.96 m s^{-1} in the previous mild-weather sampling period to 4.46 m s^{-1} during the cold wave). Nearly

identical results are obtained comparing the spatial heterogeneity in temperature and wind speed between the cold wave period and the posterior "normal" period.

Temporal and spatial variation in relative abundance of birds regarding the cold wave

The relative abundance of the three species during the cold wave did not change with respect to previous mild conditions. However, bird abundance increased after the cold wave for all species, reaching statistical significance for the blue and great tits (Figure 3 and Table 1).

The spatial variation of abundance within the forest during the cold wave was not tightly related to local temperature or wind speed, after controlling by habitat structure regarding oak height and density (Table 2). Only the relative abundance of the long-tailed tit was significantly and negatively affected by wind speed.

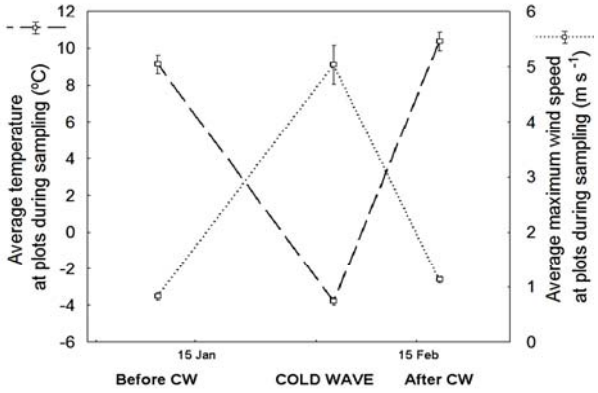

Figure 2. Decrease in temperature and increase in wind speed during the cold wave, compared with previous and post-sampling periods. Temperature (ºC) and maximum wind speed (m s^{-1}) were registered during sampling and averaged per plot and sampling period. Sample size is 15 plots. Replicates are 4 censuses per plot before the cold wave (Before CW), 7 during the cold wave (COLD WAVE) and 10 after it (After CW). X-axis shows the average sampling date of each period.

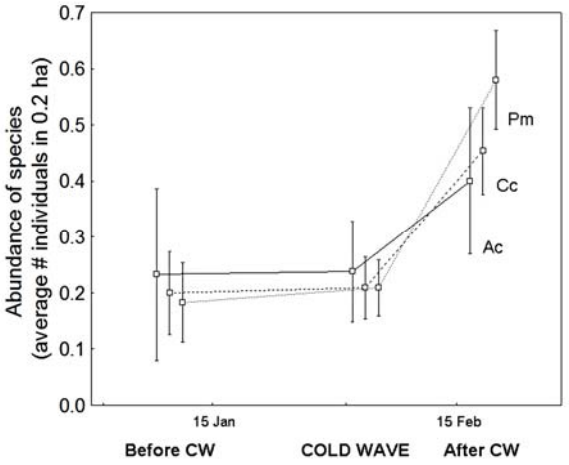

Figure 3. Abundance of birds during the cold wave, compared with previous and post-sampling periods. Abundance is the variation in the average number of individuals (+- SE) of *Aegithalos caudatus* (Ac), *Cyanistes caeruleus* (Cc) and *Parus major* (Pm) found in censuses of 5 min in 15 plots of 0.2 ha. Sample size is 15 plots. Replicates are 4 censuses per plot before the cold wave (Before CW), 7 during the cold wave (COLD WAVE) and 10 after it (After CW). X-axis shows the average sampling date of each period; the layout of abundance data of the three species is shifted for representation purposes.

Discussion

Woodland Mediterranean birds were able to cope with a winter dry cold spell that was statistically extreme in terms of the historic climate records of the region according to any measurements of temperature and wind chill. Our results clearly discard widespread mortality and temporal migration of the studied passerine populations and emphasize the character of winter residents of blue, great and long-tailed tits in Mediterranean oakwoods.

Populations may have a high ability to surpass periodic extreme events of cold weather, especially in habitats subjected to very high seasonal climatic fluctuations like the Mediterranean (average temperatures from 22ºC in summer to -5ºC in winter in Iberian oakwoods; Costa et al. 1998). Moreover, cold spells might be less damaging

Table 1. Variation in the abundance of the three species between periods. Positive figures are increases in abundance. Before CW: Mild-weather period prior to the cold wave; CW: Cold wave; After CW: Mild-weather period after the cold wave. P-values correspond to two-tailed t tests.

	Before CW to CW	p	CW to after CW	p
Aegithalos caudatus	0.00	0.929	0.16	0.173
Cyanistes caeruleus	0.01	0.947	0.24	0.003
Parus major	0.03	0.660	0.37	0.000

Table 2. Regression model on the influence of environmental factors on the abundance of *Aegithalos caudatus* (Ac), *Cyanistes caeruleus* (Cc) and *Parus major* (Pm). Figures are partial regression coefficients of average temperature and maximum wind speed after controlling by tree height and density of trees with dbh > 10 cm. P-values are two-tailed tests; significant tests are in bold type.

	Ac	p	Cc	p	Pm	p
Average temperature (ºC)	-0.013	0.934	-0.076	0.448	0.065	0.478
Maximum wind speed (ms-1)	-0.176	**0.045**	-0.048	0.398	-0.009	0.854

in the southern part of the distribution range of these Palearctic species, where the extended day length, the milder average temperatures and the higher food availability may facilitate survivorship with respect to higher latitudes (Root 2000).

Possibly, certain combinations of climate extremes might be necessary to evoke more extreme ecological responses than those found here (Smith 2011b). In this case, a dry cold spell characterized by extreme low temperatures, strong wind speeds but a low amount of precipitation was not enough to trigger a decrease in species abundance.

Snow cover and ice impede access to ground resources, and, under freezing temperatures, water from mist, rain or snow adhere to branches impeding access to food (Brotons 1997, Nakamura and Shindo 2001). Robinson et al. (2007) found that the consecutive number of snow days and cold-wet days were the variables most affecting survival of British Great and Blue tits, respectively. Moreover, Carrascal (1988) found that a snow storm provoked a significant decrease in the abundance and species richness of the avian community of a montane pinewood located in the same region. Although environmental temperatures during the snow storm were considerably higher than those registered in this study (average of -0.5 ºC with very mild wind vs 6.5 ºC during normal, sunny, winter conditions), there was a complete coverage of snow and ice in the ground, bushes and trees, which may have trigger the temporal migration of most branch- and foliage-gleaning birds along the altitudinal gradient of the mountain range. Nevertheless, snow cover and thickness was low in our study and ice crust did not affect in a generalized and widespread way the branches of the oaks. The comparison of these two studies (very cold windy weather vs. widespread cover of a thick layer of snow and ice-crust) points out that the role of temperature will be of lower importance considering that birds can withstand severe cold periods if enough food is available and its access is not completely limited (Newton 1980; Jenni 1987).

The harshness of a cold spell can be lessened by a temporal migration towards lower altitudes with ameliorated weather conditions. However, this strategy was not a possibility in our study, as the valleys below lay down only 100-200 m and the landscape was dominated by pastures, ash parklands and pinewoods, with a complete lack of oakwoods at lower altitudes within a radius of 20 km. Moreover, the cold spell was felt at a continental scale, including the whole Iberian Peninsula, and thus there were no

other places where to escape or refuge from the severe weather conditions. On the other hand, escaping to unknown areas implies a high risk considering the energy investment on small-scale migration, and the uncertainty related with the availability of food resources and competence with resident birds at the new areas (Senar and Borrás 2004). These disadvantages may prevent resident birds to move away from their regular foraging areas.

Alternatively, species may ameliorate the negative consequences of the cold wave *in situ* through various behavioral strategies. First, birds may have buffered the deleterious effects of wind chill by changing their foraging behavior, shifting to more sheltered, lower and inner parts of trees, and the leeward of substrates (Grubb 1975, 1977, Carrascal 1987, Carrascal 1988). And second, birds may selectively move locally within the forest area, searching for woodland patches where the topography and the vegetation offer higher temperatures and a greater shelter from wind (Grubb 1977, Petit 1989, Villén-Pérez et al. 2013). We indeed found that the long-tailed tit avoided the windiest plots with lowest wind chill temperatures during the cold wave (Table 2), although this search for locally milder weather conditions was not shown by the other two tit species. One explanation for the very low importance of local movements seeking for better thermal conditions is that temperature and wind conditions were much homogenized throughout the study area during the cold wave, limiting the potential benefit of spatial redistribution. This, together with the uncertainties of displacements to other locations where competition with other resident birds may increase, might prevent the role of local movements in escaping from severe weather conditions.

In summary, birds wintering in a montane forest of cold Mediterranean climate were able to resist an extreme dry cold wave, and showed no evidence of migration or widespread local mortality.

Aknowledgements

This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Education and Science. The authors thank the Navacerrada Council for the authorizations to access the study area. We also thank C. Jasinski for improving the English of the manuscript.

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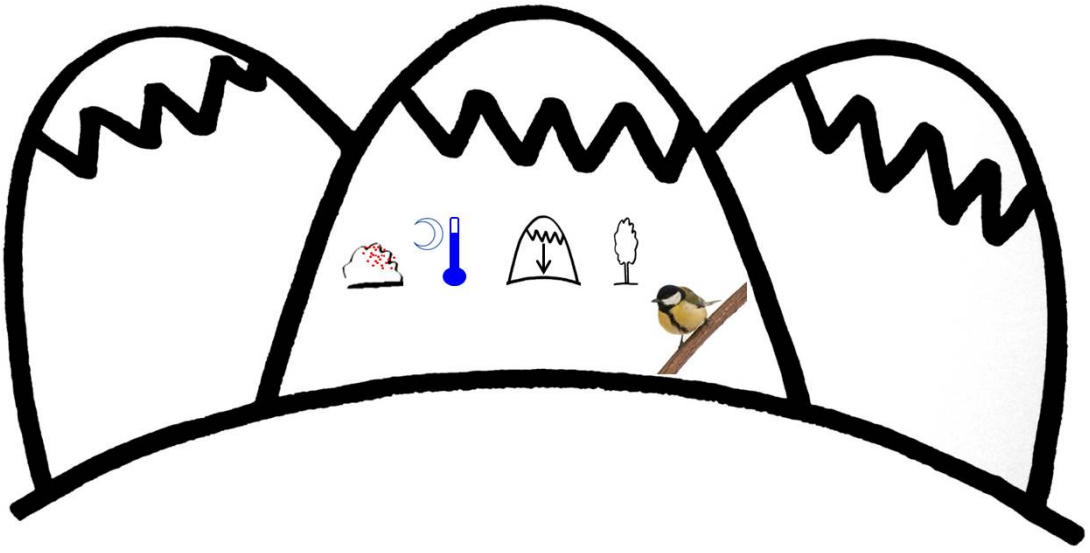
Chapter 4

Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods



Influencia del ambiente térmico, el alimento y la vegetación sobre la riqueza de especies de aves invernantes en robledales mediterráneos

Objetivo Analizar el efecto relativo del ambiente térmico, la disponibilidad de alimento y la estructura del hábitat sobre la riqueza de aves invernantes forrajeadoras en el suelo, un gremio especialmente susceptible a las condiciones invernales y las nevazones.

Localización Robledales montanos mediterráneos de la Sierra de Guadarrama (escala regional).

Métodos Durante dos inviernos consecutivos, se analiza la riqueza de especies de aves forrajeadoras en el suelo a lo largo de 20 puntos de muestreo. La temperatura se mide de forma local con registradores de temperatura, mientras que la estructura de la vegetación se estima visualmente, y la disponibilidad de artrópodos en el suelo se calcula a través de muestreos visuales exhaustivos.

Resultados y discusión La variación espacial de la riqueza de especies del gremio de los forrajeadores de suelo está determinada por la disponibilidad de alimento, pero solo para los recursos predecibles cuya disponibilidad no se ve afectada por las frecuentes nevazones (i.e., arbustos productores de frutos); mientras que la abundancia de artrópodos en el suelo tiene un efecto completamente nulo. El ambiente térmico también tiene un efecto muy importante, a través de la temperatura del aire y del mosaico sol-sombra generado por la vegetación. La riqueza de especies aumenta en las zonas de mayor temperatura nocturna, mientras que la temperatura diurna no tiene ningún efecto. Estos patrones son altamente repetibles a través de años.

Conclusiones Este trabajo destaca la necesidad de considerar los procesos fisiológicos que median las relaciones de las especies con su entorno al analizar la influencia del clima sobre la biodiversidad.

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Carrascal LM, Villén-Pérez S, Seoane J **(2012)** Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. *Ecological Research* 27: 293-302

Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods

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Abstract A better understanding of the species-energy relationship needs to be developed using fine-grained approaches that involve the use of small geographical scales of known characteristics, such as habitat heterogeneity, food availability, direct measures of temperature, and functional groups of species. We carried out a two-year study to analyze the effects of the thermal environment and food availability, while controlling for the influence of habitat structure, on winter species richness of birds living in oakwoods of a mountanious region of Central Spain of Mediterranean continental climate. The guild of ground-foraging birds was selected as model organisms considering its susceptibility to winter conditions associated to unpredictable snowfalls. The spatial variation in species richness of this guild was determined by food availability, but only for those stable and predictable resources not affected by frequent snowfalls (shrubs producing fruits; a complete lack of association was found with arthropod abundance on ground). Thermal effects directly associated with air temperature, and indirectly mediated by vegetation structure providing a mosaic of sun-shade patches, were also very influential. These patterns were highly repeatable across years. Daytime temperature had no influence determining spatial variation in species richness, but night (minimum) temperature was a very important predictor (explained considering the lower temperatures at night, the longer duration of night, and the inability of diurnal birds to develop active behavioural thermoregulation during nighttime). This result highlights the need to consider physiological processes mediating the species-environment relationships when analyzing the relationships between climatic variables and biodiversity phenomena.

Keywords: *Ground-foraging birds · Habitat structure · Mountain forests · Resource availability · Temperature*

Introduction

Global biodiversity gradients are constrained by climate throughout the influence of solar energy and water availability on trophic cascades, and the metabolic requirements of organisms (Hawkins et al. 2003; Brown et al. 2004; Qian 2010 and references therein). Nevertheless, the relationship between richness and temperature is dependent on taxonomic groups and geographic areas, is a poor predictor of observed diversity gradients in most terrestrial systems, and there is no evidence for a universal response of diversity to temperature on a broad-scale basis (Hawkins et al. 2007; Whittaker et al. 2007). A good understanding of species-energy relationships needs to be developed, mechanistically, on small geographical scales, as opposed to exploring relationships between diversity and environment with grid data cells of hundreds or thousands of square kilometers. For example, species-energy

relationships may arise because high-energy areas support more individuals, and these larger populations may buffer species from extinction, although abundant species contribute more to species-energy relationships than rare ones (Evans et al. 2005). This fine-grained approach involves using spatial units of known characteristics, such as habitat heterogeneity, food availability or direct measures of temperature, as well as differentiating among functional groups of species (i.e., guilds; see for example, Evans et al. 2006; Carnicer and Díaz-Delgado 2008; Honkanen et al. 2010).

Winter bird ranges and abundance are strongly associated with temperature (Root 1988a, 1988b; Canterbury 2002; La Sorte et al. 2009). The bases for these relationships are founded on physiological limits and on the influence of temperature on food availability. Physiological temperature limits are strongly correlated with the minimum temperature during winter at the coldest limit of the boundary range, and thus species that can tolerate cold temperatures with small relative increases in resting metabolic rate tend to be found in cold environments (Canterbury 2002). On the other hand, food availability is critical for winter survival of birds (Fretwell 1972; Newton 1980), throughout its influence on the satisfaction of energy demands, on building up body reserves to overcome fasting periods (e.g., the long winter night or during cold spells; Blem 1990; Biebach 1996), and on breeding performance the following spring (Robb et al. 2008). For example, Meehan et al. (2004) found that total abundance of wintering birds increased with environmental productivity and decreases with environmental temperature when individuals are below their thermoneutral zone (usually between 20 and 35 ºC; Calder and King 1974; Kendeigh et al. 1977). Cresswell et al. (2009) have shown that the increase of 6.5 ºC from 1995 to 2005 in mean daily winter temperature decreased the starvation risk of great tits in England (birds responded to this scenario decreasing their body mass), while Rogers and Reed (2003) showed how the ground-feeding finch *Junco hyemalis* maximize winter survival probability by integrating multiple environmental factors affecting starvation risk including temperature (but also snowfall frequency and food availability).

Ground-foraging birds are a guild susceptible to winter conditions, especially in mountain areas. Unpredictable snowfalls make food on forest floor –such as arthropods, seeds or fruits on bushes– temporally unavailable, and snow cover lasts longer at higher altitudes. On the other hand, fruit productivity and arthropod activity are lower with decreasing temperatures and solar radiation (Honek 1997; Breckle 2002). Under these circumstances, the selection of the optimal thermal environment is a basic mean of obtaining an energy balance that results from the interaction between food intake and energy expenditure (including basal, activity, digestive and thermoregulation costs). The thermal environment is determined by the interaction of numerous factors, among which temperature, wind and incidence of solar radiation stand out. Altitude is inversely related to temperature and positively with snowfall probability and persistence, although terrain effects can modify the adiabatic lapse rate (e.g., thermal inversion, exposure to sun radiation according to cardinal orientation). Solar radiation modifies the thermal environment patchily as a consequence of its incidence through vegetation screen, offering a fine-grained mosaic of shade and lit areas.

This paper analyzes the effect of the thermal environment and food availability, while controlling for the influence of habitat structure, on species richness of ground-foraging birds living in oakwoods of a mountainous region of Central Spain, using a landscape-scale approach (e.g., Turcotte and Desrochers 2005; Robb et al. 2008). The winter bird community of these forests has been previously studied (Carrascal and Díaz 2006), but food availability was not measured and the thermal environment was inferred, instead of measured, considering altitude and solar radiation according to cardinal

orientation of oakwood plots. We make two important, general, predictions explaining the spatial variation of species richness of this foraging guild. First, air temperature will be positively related to species richness, although minimum nighttime temperature will be more important than maximum daytime temperature. This contrasting pattern regarding ambient temperature may be understood considering the longer duration of night, the lower values of nighttime temperature, and the limited ability of diurnal birds to cope with thermoregulatory costs during nighttime by means of thermogenesis derived from foraging activity (i.e., heat produced during exercise, Webster and Weathers 1990; Cooper and Sonsthagen 2007). And second, spatial variation in species richness will track food availability; especially for resources whose accessibility is less prone to be constrained by unpredictable snowfalls (fruit availability in the understory should be more important than arthropods on ground).

Material and methods

Study area and period

The study area was situated in the Sierra de Guadarrama (central Spain, 40º44'N, 03º58'W), covering ca. 500 km^2. The climate of this region is continental cold Mediterranean climate, with abundant snowfalls and a large proportion of days with minimum temperatures below 0 ºC (respectively 25% and 52% of the days in December and January of the study period 2008-2010; data from 6 meteorological stations located in the study region; Spanish Agencia Estatal de Meteorología. Ministerio de Medio Ambiente, y Medio Rural y Marino). We focused on 20 oakwood plots of 75 m in diameter, located in four sectors of dense oakwoods (each sector larger than 3 km^2: La Herrería, La Golondrina, La Fuente del Cura and south slope of Morcuera Pass and north slope of Morcuera Pass), with altitudes ranging from 1000 to 1600 m asl. Though all consisting of monospecific forests of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), oakwood plots were selected to cover a wide range of variation in forest maturity, steepness and cardinal orientations of slopes and, therefore, in the amount of received solar radiation on ground. Thermal inversion is a common phenomenon in the study region (deviation from the normal negative decrease of temperature with altitude).

The study was conducted during two consecutive winters, from 01-Dec-2008 to 31-Jan-2009 and from 01-Dec-2009 to 31-Jan-2010.

Bird censuses and habitat structure

We assessed bird species richness in 20 oakwood plots using point-count stations (Bibby et al. 2000) lasting 10-min (i.e., the number of different species detected). The settlement period prior to the point count starting was 5 min. All auditory and visual contacts were recorded, but only those within a 75 m (1.77 ha) radius were used in subsequent analyses, because a large proportion (76%) of the contacts were detected within this census belt. Censuses were conducted by the same persons (LMC and JS) on nearly windless (wind speed < 3 m s^{-1}) and rainless days. We made an effort to improve accuracy in distance estimates, and to reduce inter-observer variability, by training continuously with a laser rangefinder to the cut-off point of 75 m. Plots were separated by at least 300 m to minimize the probability of sampling the same birds more than once, being the nearest oakwood plots separated by steep ridges. Average distance between oakwood plots within the four forest sectors was 1206 m (range: 300 – 3693 m), while average distance among the four forest sectors was 26.5 km (range: 8.2 – 41.3 km). Each year, the censuses were repeated in three different days during December and January (wintering season for all species), within the first 3 h of the morning and in the afternoon beginning 2 h before sunset. Thus, each oakwood plot had an accumulated

census time of 30 min, which is adequate for bird surveys of woodland birds during the non-breeding season (Shiu and Lee 2003). Species richness was measured as the average number of ground-foraging birds species per 10 min census, and bird abundance was estimated as the average of bird counts across the three censuses (expressed in birds·10 min^{-1}·1.77 ha^{-1}).

Two adjacent 25-m-radius plots were placed within each oakwood plot to sample vegetation structure, representing the total environmental heterogeneity within the census plot. Measurements defining vegetation structure were covers of the tree and shrub layers (distinguishing four bush types: oak regrowth < 2 m in height; thorny, fruit producing, shrubs of genus *Crataegus*, *Rubus, Prunus* and *Rosa*; *Cistus* spp macchie shrubs; and *Cytisus* and *Genista* brooms), average height of the shrub and tree layers, mean and number of trunks within two diameter classes: 10-30 cm and more than 30 cm at the breast level (see the Appendix for more details on habitat structure in the 20 study oakwood plots). We assumed that cover of fruiting shrubs (*Crataegus*, *Rubus, Prunus* and *Rosa*) was a surrogate of fruit availability (Shochat et al. 2002; Tellería et al. 2008). All vegetation structure variables were visually estimated, after previous training, by LMC and JS. See the Appendix for more details on ranges and mean values of habitat structure variables in the 20 study oakwood plots.

Focal species

The study species belong to a ground-foraging guild whose species spend more than 80% of feeding time on the ground (LM Carrascal, unpublished data; Cramp 1998 for general details; Carrascal et al. 1987 for this group of species in forests of Central Spain). The species included are (in decreasing order of abundance): blackbird, *Turdus merula* (average of 0.25 birds per oakwood plot in the two study winters); mistle thrush, *Turdus viscivorus* (0.24); redwing, *Turdus iliacus* (0.22); european robin, *Erithacus rubecula* (0.16); chaffinch, *Fringilla coelebs* (0.14); eurasian wren, *Troglodytes troglodytes* (0.13); song thrush, *Turdus philomelos* (0.09); citril bunting, *Emberiza cirlus* (0.05); rock bunting, *Emberiza cia* (0.04); dunnock, *Prunella modularis* (0.03); black redstar, *Phoenicurus ochruros* (0.02). The majority of these birds are facultative frugivores that also include a large proportion of invertebrates in their diets (*Turdus merula*, *Turdus viscivorus*, *Turdus iliacus*, *Erithacus rubecula* and *Turdus philomelos*; Guitián 1985; Cramp 1998; these five species account for 70% of all detected individual birds in the censuses carried out in the 20 woodland plots). A considerably smaller proportion of birds wintering in these oakwoods rely mainly or exclusively on seeds or vegetal matter (*Fringilla coelebs*, *Emberiza cirlus*, *Emberiza cia* and *Prunella modularis*; 19% of all detected individual birds in the censuses). Finally, only *Troglodytes troglodytes* and *Phoenicurus ochruros* were mainly insectivorous species (11% of all birds counted).

Air temperatures

To describe winter air temperature we set one temperature logger (Onset HOBO Pendant) in each oakwood plot, placed on thick trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every ten minutes from 01-Dec-2008 to 31-Jan-2009 and from 01-Dec-2009 to 31-Jan-2009. For each recording day (144 measurements) we obtained average temperature, average daytime temperature, average night temperature, maximum daytime temperature and minimum night temperature. Temperatures for the 62 days of the study period were averaged for each oakwood plot. All these five temperature measurements were highly correlated across days and oakwood plots. Thus, and in order to avoid multicollinearity in data analyses, we selected the two least correlated measurements: minimum night and maximum daytime temperature. Moreover, these two temperatures have a clear functional meaning

related, respectively, to maximum thermoregulatory costs at night and minimum thermoregulatory costs at daytime.

Operative temperature and radiation on the ground

As an approximation to the operative temperature experienced by foraging birds on the ground, we used hollow copper cylinders (length 5 cm, diameter 1 cm) closed at both ends except for a small fissure that allowed us to insert the sensing tip of an electronic digital thermometer (digi-thermo; $\pm$0.1 ºC precision). On calm days, this environmental temperature integrates all the exogenous heat sources influencing a foraging bird: radiation from the sun, conduction from the substrate and the effect of wind on thermal conductance. We assume that these devices indicate the temperature a bird would eventually reach if it did not have metabolic heat production. Previous measurements showed that copper cylinders and taxidermic mounts (copper models covered by passerine skins) eventually reached the same equilibrium temperatures (see Carrascal et al. 2001 and references therein for more details on the application of this technique to small forest bird species).

We selected 30 sampling points centered in the study area (Biological Station of El Ventorrillo) that were sampled within seven hours around the zenit of cloudless and windless days. In each sampling point we set two electronic digital thermometer-hollow copper cylinders five cm above the forest floor separated 25-50 cm, one exposed to direct sun radiation and another in deep shade (e.g. on a trunk shade). We distributed the two thermometer-hollow copper cylinders so that they sampled the whole variability in radiation intensity in the study forest on six different days (14th January to 10th February). We also sampled air temperature at the same place using another thermometer-hollow copper cylinder (located 1.5 m above ground, in the shade). Environmental temperatures were registered three minutes after hollow copper cylinders were settled five cm above the ground, to assure temperature measures were stabilized, and checking for its stability during the next minute. Radiation intensity was also measured at each sampling point with a PAR light sensor (Quantum QSO, measuring radiation from 400 to 700 nm). At the end of the 3-min periods, we took 12 radiation measurements at 5-s intervals in the same position where the thermometer-hollow copper cylinders were placed (incident radiation was estimated as the average of these 12 measurements). Variation in operative temperature was analyzed with a GLM regression model using air temperature and radiation as predictor variables.

Arthropod availability on ground

Prey availability for ground-foraging species was estimated by counting all arthropods longer than 1 mm found during visual searches of 2 min on patches of 50x50 cm^2 (see Cooper and Whitmore 1990 and references therein). Counts were made in winter 2009-2010 from 10 a.m. to 5 p.m., when temperatures reached higher values for arthropods to be active. Ground patches were mainly composed of oak litter and were dry and clean of snow during sampling. Arthropods were searched on the surface of the ground because the study species are ground gleaners that do not dig or remove oak litter while foraging for arthropods. Twenty patches were sampled in each oakwood plot within 50 m from their centers. All prey items were identified to order and estimated to the nearest millimeter *in situ* without collecting them. Dry body masses were estimated using the allometric equations available in Díaz and Díaz (1991). No arthropods were found in 40.2% of the patches. Average encounter rate with arthropods was 1.29 arthropods / 2 min (n=400 2-min samples). The average length of the encountered arthropods was 3.78 mm (n=515 individuals), with and average dry mass of 2.02 mg. The main arthropod groups were Hemiptera, which accounted for 47.6% of total individuals, Arachnids 20.6%,

Orthoptera 8.7%, Diptera 6.2%, Coleoptera 5.0%, and Hymenoptera 4.9%.

Data analyses

The relationships between the response variable (species richness, i.e., average number of ground-foraging birds species per 10 min census in winter 2009-2010) and habitat structure variables, temperatures and arthropod availability (predictors) were analysed by means of Partial Least Squares Regressions (hereafter PLSR; Abdi 2007), using oakwood plots as sample units. Results obtained with PLSR are similar to those from conventional multiple regression techniques; however, it is extremely robust to the effects of sample size and degree of correlation between predictor variables, which makes PLSR especially useful in cases of low sample size and severe multicollinearity (Carrascal et al. 2009). Associations with the response variable are established with factors extracted from predictor variables that maximize the explained variance in the dependent variable. These factors are defined as linear combinations of independent variables, so the original multidimensionality is reduced to a lower number of orthogonal factors to detect structure in the relationships between predictor variables and between these factors and the response variable. The extracted factors account for successively lower proportions of original variance. The relative contribution of each variable to the derived factors was calculated by means of the square of predictor weights. Only those components significant after a five-fold validation procedure were retained.

Although only the results for average species richness of the study species are presented, very similar results are obtained when analyzing data for the cumulative number of species in the three censuses per oakwood plot, and the three most abundant species. Therefore, and for the sake of brevity, we avoid the presentation of these results.

Variation in operative temperature 5 cm above ground was analyzed by means of a multiple regression, using solar radiation and air temperature (in the shade) as predictor variables. Other statistical procedures used were paired t-tests, Pearson correlations, and parallelism test (applying one-way ANCOVA with the two study winters as factor). All the statistical analyses were carried out using Statistica 9.0 (StatSoft Inc., Tulsa, Oklahoma).

Results

Air temperatures

The lowest minimum night temperatures in the 20 oakwood plots ranged between -16.7 and -7.5 ºC, while the maximum daytime temperatures ranged between 12.8 and 19.4 ºC (see the Appendix for more details on ranges and mean air temperatures in the 20 oakwood plots). Thus, temperature throughout the study period was constantly below the lower critical temperature, outside the thermoneutral range for a small passerine (usually below 18 to 22 ºC for many winter acclimated species in temperate areas; Calder & King 1974; Kendeigh et al. 1977). That is, the studied birds faced an environment that probably required regulatory thermogenesis much of the time.

Variation in operative temperature on the ground

Average operative temperature 5 cm above ground under direct solar radiation was 23.1 ºC (sd = 6.06, n=30) in cloudless days from 10 h a.m to 5 h p.m., while it decreased to 12.7 ºC in the shade (sd = 2.16, n=30). These temperatures were recorded under a broad variability in air temperature (-0.5 to 16 ºC). The highest recorded operative temperature exposed to full sun at midday was 34.3 ºC in a warm winter day when air temperature was 13.9 ºC. The average difference in operative temperatures 5 cm above ground between full sun – shade

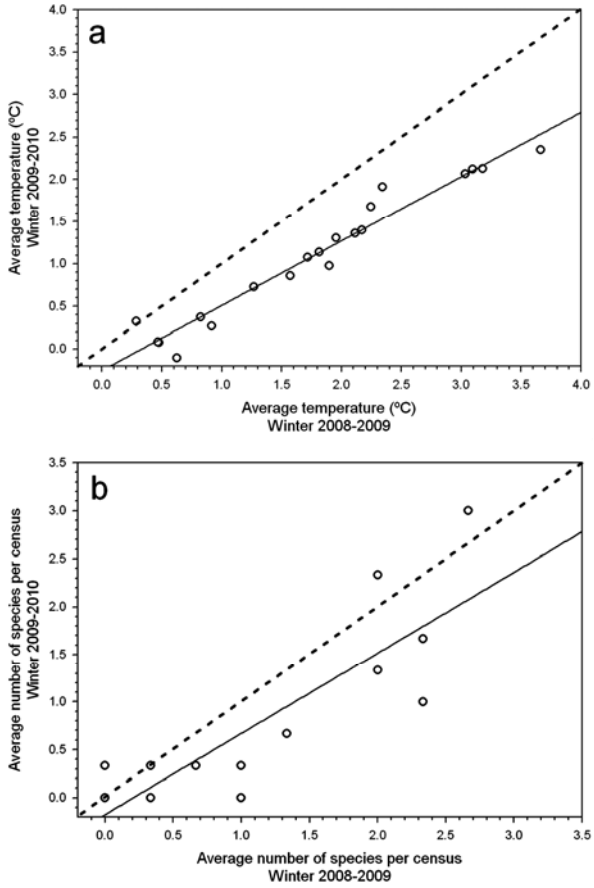

Figure 1. Relationship between a) average temperature and b) average number of species per census in winters (December - January) 2008-2009 and 2009-2010 in Central Spain. The study species are *Emberiza cirlus*, *E. cia*, *Erithacus rubecula*, *Fringilla coelebs*, *Phoenicurus ochruros*, *Prunella modularis*, *Troglodytes troglodytes*, *Turdus iliacus*, *T. merula*, *T. philomelos* and *T. viscivorus*. Sample size is 20 oakwood plots and p-values are P=0.0000 in both cases. Dashed line denotes what would be the identity between measures in both years; continuous line is the regression line between data in the two study winters.

exposition was 10.4 ºC, with a relatively low coefficient of variation (43.7 %). Therefore, birds foraging on the ground exposed to direct sun radiation, instead of on the ground in deep shade, obtained a considerable thermal benefit during winter in the study oakwoods.

Operative temperature 5 cm above ground was a very deterministic phenomenon (R^2 = 89.2%; F = 235.2, df = 2, 57, P<<0.001). Solar radiation was the most important factor explaining variation in operative temperature (standardized regression coefficient, beta = 0.86, P<<0.001; partial effect: 70.4% of variance). Air temperature (in the shade) was also significantly and positively associated with operative temperature (beta = 0.23, P<<0.001; partial effect: 4.8% of variance).

Variation in species richness and microclimate across woodlands and years

Average air temperature was highly correlated with minimum night temperature across oakwood plots in the two study winters 2008-2009 and 2009-2010 (Pearson correlation coefficients are, respectively, 0.975 and 0.972, n=20 and P<<0.001). Average temperature reached significantly lower figures in winter 2009-2010 than in 2008-2009; 0.68 ºC lower in 2009-2010; 95% confidence interval: 0.54 – 0.81 ºC (paired t-test: P<<0.001; Figure 1A).

Average number of ground-foraging species per oakwood plot was highly and significantly correlated in the two study winters (r=0.873, n=20, P<0.001). The same

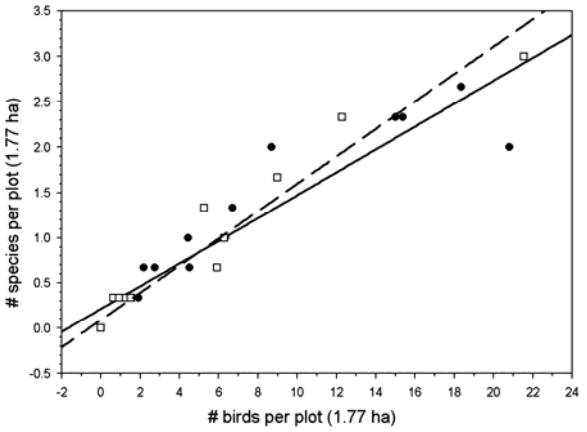

Figure 2. Relationship between species richness and bird abundance of ground-foraging birds per woodland plot of 1.77 ha in two consecutive winters in Central Spain. Dots and continuous line: winter (December - January) 2008-2009. Box and dashed line: 2009-2010. Data refers to the average of three censuses in 20 woodland plots. Several data points are completely overlapped.

result was obtained for the accumulated number of species detected in the three censuses (r=0.793, P<0.001). Species richness was significantly lower in winter 2009-2010 than in 2008-2009 for both average number of species per census (Figure 1B) and the accumulated number of ground-foraging species (P<0.005 in the two paired t-tests).

In summary, differences in microclimatic conditions and bird species richness among oakwood plots were repeatable across years. Number of ground-foraging species per plot was lower in the colder and cloudier winter (2009-2010) than in the warmer and sunnier one (2008-2009).

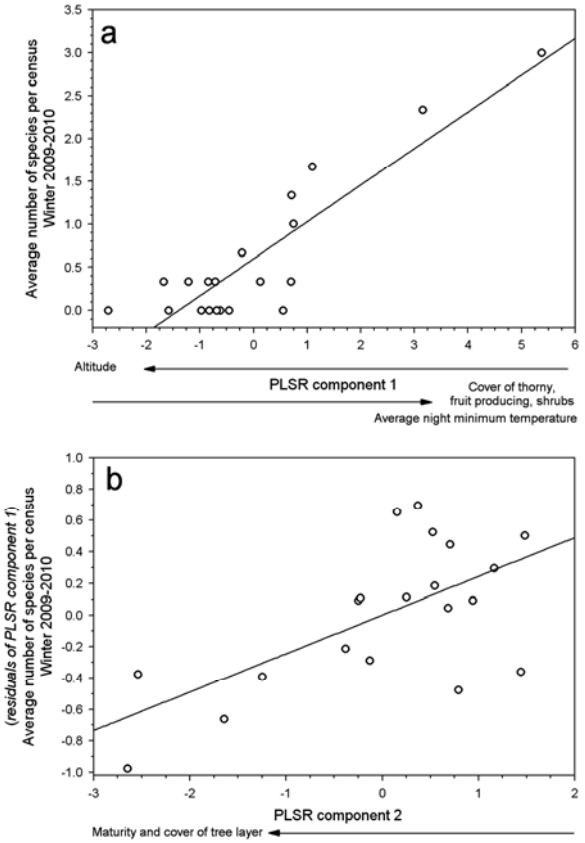

Figure 3. Relationship between ground-foraging species richness and the two first components of a partial least squares regression analysis (PLSR; see Table 1). The b) second PLSR component; analyzes the residuals of the relationship depicted by the a) first PLSR component, according to the sequential variance extraction carried out by PLSR models. Sample size is 20 oakwood plots located in Central Spain in winter 2009-2010 and p-values are P=0.0026 and P=0.0000, respectively

Spatial variation in species richness of ground-foraging birds

Species richness and abundance of ground-foraging birds were highly correlated in both study winters: r=0.942 for winter 2008-2009 and r=0.974 for winter 2009-2010 (n=20 woodland plots and P<0.001 for both correlations; Figure 2). The regression slopes did not significantly differ between winters 2008-2009 and 2009-2010 (parallelism test: $F_{1,36}$=3.14, P=0.09). Therefore, species richness increases just because there are more individuals, and this pattern did not change between consecutive winters.

Two significant components, accounting for 87.5% of total variance in species richness, were obtained in the PLSR analysis with the 20 oakwood plots in winter 2009-2010, when arthropod availability was sampled (Table 1). Residuals of this PLSR model did not differ among the four forest sectors ($F_{3,16}$=2.47, P=0.1). The most influential variables in this PLSR model were cover of thorny, fruit producing, shrubs, average night minimum temperature, altitude, density of large and medium sized oaks (trunk diameter at breast height >30 cm and 10-30 cm, respectively), and oak average height (i.e., they summarized 90.6% of the information content of predictor variables explaining ground-foraging species richness; percentage obtained adding the squares of variable importances in Table 1). Conversely, diurnal maximum temperature and arthropod availability on ground had no influence explaining inter-plot differences in species richness (see variable importances in Table 1).

The first PLSR component (79.1% of variance, P<<0.001) was positively associated with cover of thorny shrubs producing fruits and minimum night temperature, while it was negatively related to altitude (these three variables were responsible of 75.2% of the information content of this component). Thus, oakwood plots located at lower altitudes, with a dense cover of thorny shrubs producing fruits, and

Table 1: Results of the partial least squares regression (PLSR) model explaining species richness of ground-foraging birds in 20 oakwood plots in Central Spain in winter 2009-2010. VarImp: variable importance in the PLSR model with two components. Figures under PLSR-1 and PLSR-2 are the predictor weights of each variable in each component; only relationships between individual variables and PLSR components with |weights|>0.3 are shown

	VarImp	PLSR-1	PLSR-2
Cover of thorny, fruit producing, shrubs	0.513	0.53	
Average minimum night temperature	0.465	0.48	
Altitude	0.463	-0.49	
Density of large sized oaks (trunks > 30 cm dbh)	0.312		-0.45
Density of medium sized oaks (trunks 10-30 cm dbh)	0.248		
Average oak height	0.231		-0.46
Tree layer cover	0.170		-0.34
Cover of Cytisus and Genista shrubs	0.169		
Average shrub layer height	0.116		
Cover of oak regrowth (< 2 m in height)	0.096		-0.30
Average maximum diurnal temperature	0.085		
Cover of Cistus spp shrubs	0.075		
Arthropod biomass on ground	0.028		
R^2 by PLSR components		0.791	0.085

with higher minimum night temperatures had higher number of species foraging on the ground (Figure 3). The second PLSR component, although quantitatively of lower importance (8.5% of variance, P=0.003), was mainly related (negatively) to oak cover (both tree and regrowth layers), average tree height, and density of medium sized oaks. Thus, species richness of ground-foraging birds decreased with maturity and development of the tree layer and cover of oak regrowth: mature and dense oakwoods plots maintained a lower number of species of this foraging guild.

Discussion

Abiotic effects of temperature and altitude

Our results show that temperature plays an important role in determining the spatial variation in species richness of this guild of ground-foragers during winter. Moreover, this within-year pattern is also observed in the between-year analysis: the number of ground-foraging species per oakwood plot is lower in the colder winter despite between-years difference in average air temperature is as low as 0.68 ºC. The mechanistic link between species richness and temperature can be understood as a deterministic outcome of physiological processes, because temperature affects the metabolism of individuals, and species richness increases just because there are more individuals per woodland plot (see Figure 2). Low temperatures and long nights of winter are associated with an increased risk of starvation through body reserves regulation (e.g., Cresswell 1998; Gosler 2002; Macleod et al. 2005; Krams et al. 2010). Temperature determines metabolic expenditure of birds below the thermoneutral zone, the lower limit being around 20 ºC for many winter acclimated species in temperate areas (Calder and King 1974; Kendeigh et al. 1977). Temperature in our study area is considerably lower than the lower critical temperature, ranging from 4.5 to 8.9 ºC for average maximum diurnal temperature, and -3.2 to 1.2 ºC for average minimum nocturnal temperature. Thus, overwintering in these continental Mediterranean oakwoods is

energetically demanding in terms of thermoregulatory metabolic costs.

Nevertheless, winter temperature has a different meaning for this group of birds depending upon what temperature is considered. Daytime (maximum) temperature has no influence explaining spatial variation in species richness, but night (minimum) temperature is a very important predictor according to its variable importance in the PLSR analysis. This contrasting pattern of covariation with species richness may be easily explained considering the low temperatures attained during night and the considerably longer duration of night (average duration of night: day during the study period = 14.4 h : 9.6 h). Whenever not sleeping, heat production resulting from locomotor muscles during foraging activity and from food assimilation, can account for part of thermoregulatory requirements in the cold for diving, glean-and-hang foraging species, as well as in ground-foraging birds (Webster and Weathers 1990; Dawson and O'Connor 1996; Kaseloo and Lovvorn 2006; Cooper and Sonsthagen 2007). On the other hand, small passerines are able to compensate for low air temperatures behaviourally, by spending more time in sunlit patches while foraging (Carrascal et al. 2001). The contrasting effects of temperature on bird species richness suggest the need to consider with caution any attempt to relate climatic variables to biological phenomena simplistically, with disregard to the autoecological and physiological processes mediating the species-environment relationships.

Finally, the great negative influence of altitude determining the observed pattern of species richness is probably a combination of temperature (discussed above) and snow-mediated effects. Snow cover forces birds to shift their foraging behaviour or migrate (Brotons 1997; Nakamura and Shindo 2001); thus, snowfall frequency and persistence may be considered as a surrogate measure of resource deterioration. At higher altitudes, snowfall probability increases while snow cover lasts longer, constraining food searching on the ground, and thus determining the observed reduction in species richness with altitude.

Biotic effects of vegetation structure and food resources

Food availability has been proposed to drive winter distribution in small birds (see review in Newton 1980; Wiens 1989), although its effect depends on the ability of birds to efficiently track its spatio-temporal distribution (Shochat et al. 2002). A greater abundance of food resources would reduce the amount of time required for searching during the few light hours of winter days, and increase the rate of food intake in order not to starve. Therefore, food abundance should be an important factor determining population density and habitat selection through foraging efficiency. Nevertheless, previous research with both frugivorous and insectivorous birds have reported a mixed bag of results, as in some studies food abundance has been found to be important whereas in other studies its effect was negligible (see examples for the Iberian Peninsula in Herrera 1998; Carrascal et al. 2001; García and Ortiz-Pulido 2004; Tellería and Pérez-Tris 2003, 2007; Tellería et al. 2008).

Resources like arthropods or seeds on the forest floor of Pyrenean oakwoods are scarce and highly unpredictable for ground-foraging birds living in mountainous areas, where snowfalls severely constrain its accessibility. In winter, the grass layer is nearly absent in these forests, and the seed bank produced during summer is completely covered by a dense layer of leaves fallen during autumn. This is the reason why granivorous birds are so scarce in dense deciduous forests during winter in the Mediterranean region (Tellería et al. 1988). On the other hand, arthropods are very scarce according to a very low encountering rate with them (1.29 arthropods / 2 min) and their average low body masses (dry mass of 2.02 mg). These facts, together with the impossibility of having a sure access to this

resource throughout the winter due to snowfall unpredictability, could explain the almost null effect of arthropod biomass on species richness found in this study.

Conversely, cover of fruit producing shrubs (as a surrogate of fruit availability) is the best predictor of species richness of ground-foraging bird in the Pyrenean oakwoods, indicating that this group of species (mainly dominated by facultative frugivorous species) is food limited during winter time and that they track the spatial patterning of fruit producing shrubs (see also Guitián and Munilla 2008 and Tellería et al. 2008 for bird and fruit abundance in scrublands and woodlands of northern and southern Spain). The cover of other shrubs does not exert any influence on species richnness of ground-foraging birds. Snow cover scarcely affects availability of fruits in shrubs, which could in turn be a highly predictable food resource. On the other hand, as these fruit producing shrubs (*Rosa*, *Prunus*, *Crataegus*, *Rubus* species) are thorny and grow in dense patches, they may play an additional role providing protection against predators while foraging on the ground.

Other habitat structure variable related to bird species richness is tree maturity (tree thickness, cover and height), explaining a considerably lower amount of variance. Nevertheless, and in contrast with other bird guilds for which positive relationships have been found (e.g., Turcotte and Desrochers 2005; Carrascal and Díaz 2006; Godinho et al. 2010; Honkanen et al. 2010), species richness of ground-foraging birds decreases with maturity and development of the tree layer. The unexpected negative influence of forest maturity on bird species richness of this foraging guild may be explained by considering the detrimental effect of shadow projection on thermoregulation during normal foraging activities on forest floor: mature forests have a well developed tree crown projecting more shadows where operative temperatures are considerably lower than in patches with incident sun radiation (see Carrascal et al. 2001 for empirical evidence on behavioural patch selection with *Certhia brachydactyla*). Operative temperature on ground is very predictable, and the received sun radiation explains 70% of its variation. Thus, the thermal benefit obtained by a bird staying on ground exposed to sun instead of in the shade is, on average, 10.4 ºC. Complementarily, this increased temperature could have a positive, indirect, effect on foraging efficiency through the activation of arthropods at higher temperatures (Avery and Krebs 1984; Carrascal et al. 2001), which would lead birds in sunlit patches to achieve higher foraging success. Therefore, small-scale effects mediated by the interaction sun radiation - vegetation structure may enhance the role of the thermal state of the environment on bird species richness.

In conclusion, regional variation of small scale (~1-2 ha) species richness of the ground-foraging guild of birds wintering in oakwoods of mountainous areas in Central Spain is mainly determined by cover of fruit producing shrubs followed by thermal effects, directly associated with minimum temperature during the long winter nights. Thus, food availability is very influential, but only for those stable and predictable resources (shrubs producing fruits), not affected by frequent snowfalls (i.e., null influence of arthropods on ground). These patterns are highly repeatable across years, and support the species-energy relationship at small spatial scales, as high-energy areas with higher temperatures and more resources (fruits) support larger bird abundances that buffer species from local disappearance. The marked difference in the influence of diurnal (null) and nocturnal (very positive) temperatures on the regional variation in species richness highlights the need to consider physiological processes mediating the species-environment relationships when analyzing the relationships between climatic variables and biodiversity phenomena.

Acknowledgements

This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Educación y

Ciencia. We also thank Claire Jasinski for improving the English of the manuscript.

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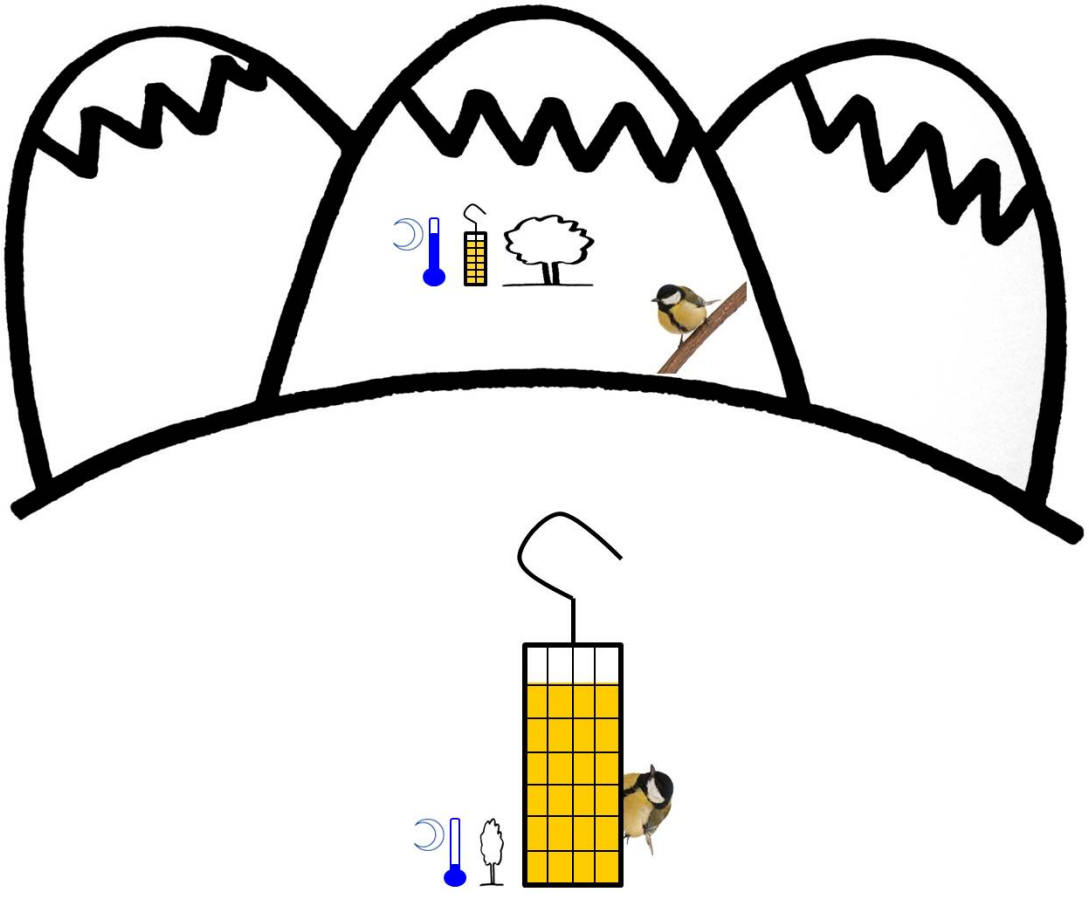
Chapter 5

Temperature and food constraints in wintering birds - an experimental approach in montane Mediterranean oakwoods



Restricciones de la temperatura y el alimento en aves invernantes – una aproximación experimental en robledales mediterráneos montanos

Objetivo Analizar el efecto relativo de dos medidas de energía distintas sobre la distribución de aves invernantes en una aproximación de "grano fino". En concreto, discernir los efectos del alimento (relacionado con el aporte de energía) y de la temperatura (relacionada con el gasto metabólico de termorregulación) sobre la abundancia de aves.

Localización Robledales montanos mediterráneos de la Sierra de Guadarrama (escala regional).

Métodos Se analiza la abundancia de aves del gremio de las forrajeadoras arbóreas a lo largo de 40 puntos de muestreo. En la mitad de estos puntos se colocan fuentes suplementarias de alimento (i.e., comederos). La temperatura se mide de forma local con registradores de temperatura y la estructura de la vegetación se estima de forma visual. Además, se analizan los determinantes ambientales de la variación en el consumo del alimento suplementario.

Resultados y discusión La variación espacial en la abundancia de forrajeadores arbóreos se relaciona positivamente con ambos componentes energéticos (temperatura y fuentes de alimento suplementario), a pesar de encontrarnos en bosques mediterráneos del sur de Europa con un clima relativamente benigno. La variación espacial en el consumo de alimento suplementario se relaciona negativamente con la temperatura y está mediada por la estructura de la vegetación, disminuyendo con la madurez del arbolado.

Conclusiones Este trabajo señala que la disponibilidad de energía es más importante que la estructura del hábitat determinando la abundancia invernal de las aves forrajeadoras arbóreas.

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Carrascal LM, Seoane J, Villén-Pérez S **(2012)** Temperature and food constraints in wintering birds - an experimental approach in montane Mediterranean oakwoods. *Community Ecology* 13(2): 221-229

Temperature and food constraints in wintering birds - an experimental approach in montane Mediterranean oakwoods

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Abstract Although energy is a major driver of global patterns of biodiversity and species distribution, the test of species-energy relationships needs further development using fine-grained approaches involving different functional groups of species and small geographical scales of known characteristics (habitat heterogeneity, food availability, direct measures of temperature). We carried out an experiment over a broad range of habitat structure and environmental conditions to disentangle the effects of two different energy measures on the small-scale variation of habitat use in winter: one directly related to food resources (manipulated food availability with artificial feeders), and another related to thermoregulatory costs (night temperature). The spatial variation in abundance of a guild of tree-gleaning birds wintering in montane Mediterranean oakwoods of Central Spain was positively related to both components of energy availability (temperature and food resources), even in these Mediterranean montane forests of southern Europe of relatively mild climate. Spatial variation in consumption of food from artificial feeders was negatively related to spatial variation in temperature. The influence of food availability on bird abundance was mediated by vegetation structure, with a lower influence in maturer oakwoods. This study highlights the important role of the energy-related factors, over habitat structure, in determining winter abundance of the studied tree-gleaning guild.

Keywords: B*ird density · Mountain forests · Food abundance · Thermal environment · Winter*

Introduction

A major explanation for current global patterns of biodiversity, and for predictions of its future alterations under climate change, is given by the set of hypotheses based on energy availability (Hawkins et al. 2003, Pimm and Brown 2004). Energy availability is associated with temperature, radiation and food resources, and has been shown to influence patterns of species richness or community structure at a range of spatial and temporal scales across several taxa (e.g. Lennon et al. 2000, Hurlbert 2004, Evans et al. 2006). At northern and high elevation range margins, energy availability is the single best factor to explain species richness (Whittaker et al. 2003), and it is commonly argued that temperature is the single most important abiotic environmental factor that affects the performance of organisms and determines the distribution of species (but see Clarke and Gaston 2006). Thus, climatic conditions influence the dynamics of animal populations (e.g. Newton 1998 for birds). In fact, there is a great deal of evidence of the influence of the recent increase in ambient temperatures on the breeding biology of many bird species, both at local and large spatial scales (e.g. Saether et al. 2003, Sanz 2002, Sanz et al. 2003, Visser 2008). Nevertheless, and although temperature is

often an important abiotic predictor, its influence may be not necessarily exerted through a direct process, which is particularly true for species with thermoregulatory abilities like birds (e.g., Suggitt et al. 2011).

Meehan et al. (2004) emphasized the importance of individual energetics for understanding these macroecological patterns with a general theoretical model validated with bird data. They found that total abundance of wintering birds increases with environmental temperature and productivity when individuals are below their thermoneutral zone. Zuckerberg et al. (2011) found that average minimum temperature was an important factor limiting winter bird distributions in north-eastern North America, supporting the hypothesis that the occupancy of wintering birds is limited by climatic constraints. These patterns agree with the long-held view that there is a ceiling on metabolic rate that constrains the northern winter distributions of bird species, and that such constraint predominates over other biotic processes that might also influence distributions (Root 1988). Nonetheless, Repasky (1991) found little evidence to support that the northern distributions of wintering birds are governed principally by temperature. He argued that temperature probably plays a role in determining distributions through interactions with biotic factors such as food, habitat structure and competition, reinforcing the importance of considering the interaction between temperature and resource availability; that is, between the costs faced by individuals in cold environments and the capacity to overcome these costs.

In spite of these broad-scale spatial patterns of animal numbers, species richness and distribution limits, there are few studies dealing with smaller scales and under less contrasting scenarios according to habitat type and heterogeneity. Wintering birds are suitable organisms to investigate the relative importance of energy and resource constraints in determining the structure of assemblages at local scales and their response to climate change. Winter is the season that arguably affects bird populations that reside year-round in the northern hemisphere, as they appear to be energy limited in this season (Fretwell 1972). Winter survival depends primarily on obtaining enough food for self-maintenance (e.g. Newton 1998, Macleod et al. 2005, Cresswell 2008, Cresswell et al. 2010). Winter climatic conditions do appear to influence overwinter survival of bird populations that reside year-round at northern latitudes of harsh climate through the direct effects on temperature-related mortality or indirectly via food availability (e.g. Lahti et al. 1998, Doherty and Grubb 2002). Temperature acts as a proximate factor influencing fat reserve levels (e.g. Gosler 1996, Rogers and Reed 2003), even in the short term, as the more immediate temperatures (e.g. < 5 h) may be used to optimize fat reserves (see Gosler 2002 for Great Tit, *Parus major*). As a consequence, higher temperatures may reduce energy demands (Calder and King 1974) and are likely to improve the quality of the winter foraging environment (e.g. Dolby and Grubb 1999, Cresswell et al. 2009). Moreover, climate influences on food availability may provide the mechanism by which populations change under different climatic conditions (Robinson et al. 2007).

Here we set out to disentangle the effects of temperature and food availability on the local abundance of birds wintering in Mediterranean oakwoods of the Iberian Peninsula. Although several studies have dealt with forest bird communities along biotic and abiotic gradients during winter in this region (see review by Senar and Borras 2004; Carrascal and Díaz 2006), the role of food availability structuring bird assemblage has been measured or manipulated in very few occasions, and the influence of the thermal environment has been indirectly inferred considering altitude and incidence of solar radiation. Our fine-grained approach involves spatial units of known characteristics, such as habitat heterogeneity, food availability or direct measures of temperature, using a particular functional

group of species: the tree-gleaning guild (see for example, Evans et al. 2006; Carnicer & Díaz-Delgado 2008; Honkanen et al. 2010). We carry out a landscape-scale experiment focusing on a homogeneous guild of tree-gleaning birds wintering in continental Mediterranean oakwoods of Central Spain, using two different energy measures: one related to thermoregulatory costs (night temperature) and the other accounting for resources (experimentally manipulated food availability by large-scale diffuse feeding of populations; e.g. Turcotte and Desrochers 2005, Robb et al. 2008, Zuckerberg et al. 2011). The experimental provisioning with supplemental food and the fine-grained measurements of temperature were carried out at local scale of forest patches, over a broad range of altitudes, cardinal orientations and habitat structure deliberately obtained by means of random and systematical sampling of oakwood forests of *Quercus pyrenaica*. We test three general predictions: the small-scale variation of bird abundance in winter (a) will be positively associated with temperature and (b) will increase with the experimental addition of supplementary food, because higher food availability and temperatures facilitate keeping a suitable energy balance. And finally, (c) winter consumption of supplemented food will be negatively related to temperature.

Material and methods

Study area and species

The study was conducted during the winter of 2009-2010 in the Sierra de Guadarrama (Madrid province, Central Spain, 40º54'11" – 40º33'45"N, 3º46'08" – 4º10'03"W), spanning over 500 km^2 at altitudes ranging from 900 to 1600 m asl. The region has a continental cold Mediterranean climate, with abundant snowfalls and a large proportion of days with minimum temperatures below 0ºC (respectively 25% and 52% of the days in December and January of the study period 2009-2010; data from 6 meteorological stations located in the study region kindly provided by the Spanish Instituto Nacional de Meteorología). Forty census stations were selected in oakwood forests of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), within forest tracts larger than 3 km^2 in order to avoid the probable influence of fragmentation in forest bird assemblages (e.g., Tellería and Santos 1995, Battisti et al. 2009 for the Mediterranean region). They covered a wide range of variation in forest maturity, habitat structure due to their management system, altitude and steepness and cardinal orientations of slopes (to account for the amount of incident solar radiation). They were georeferenced with a GPS, and located at least 400 m apart within the same area (the nearest census plots were separated by steep ridges). Twenty of these census stations were randomly selected and food-supplemented with feeders.

The study species were those belonging to the tree-gleaning guild of the mountainous forests of central Spain (Carrascal and Díaz 2006) that have omnivorous diets (Perrins 1998): *Sitta europaea* (Nuthatch), *Parus major* (Great Tit), and *Cyanistes caeruleus* (Blue Tit). These small-sized species mainly forage in the foliage, twigs and branches of trees, although they can also use the forest floor or trunks as foraging substrates (especially Nuthatch). In addition, they are regular exploiters of artificial feeders in the study region (e.g. Carrascal and Alonso 2006). Frequent opportunistic observations at feeders during the study period (while censusing birds or checking feeders for depletion) showed that these species were using the supplemental food during the winter. Three other species make use of artificial feeders in the forests of the study region (see Carrascal and Alonso 2006), but were either very scarce or not detected in the studied woodlands (coal tit, *Periparus ater*, and crested tit, *Lophophanes cristatus*, two coniferous specialist), or do not regularly exploit these feeders due to its bill size (long-tailed tit, *Aegithalos caudatus*). As for other

Table 1. Mean and sd of study variables in 40 oakwood census plots in Central Spain during winter (20 control plots and 20 plots supplemented with peanuts). Temperatures for the 62 days of the study period were averaged for each oakwood plot. Density of individual birds per plot refers to the average of three censuses in plots 75 m in radious (i.e., distances to birds truncated to 75 m).

	range	*n* = 40	CONTROL		SUPPLEMENTED	
	min - max	mean	mean	sd	mean	sd
Average bird density (birds / 1 ha)	0.0 – 12.8	5.2	3.9	3.0	6.5	3.3
Nuthatch (*Sitta europaea*) density	0.0 – 8.1	2.3	1.8	1.9	2.8	2.2
Great Tit (*Parus major*) density	0.0 – 4.3	1.2	0.9	1.1	1.5	1.1
Blue Tit (*Cyanistes caeruleus*) density	0.0 – 5.4	1.7	1.3	1.3	2.2	1.6
Altitude (m)	965 - 1589	1260.0	1238.4	146.6	1281.5	167.5
Average air temperature (ºC)	1.0 – 3.6	2.3	2.3	0.8	2.3	0.7
Average diurnal temperature (ºC)	2.4 – 5.5	4.0	4.0	0.8	4.0	0.7
Average maximum temperature (ºC)	4.8 – 8.2	6.8	6.8	0.9	6.9	0.8
Average night temperature (ºC)	-0.1 – 2.5	1.2	1.2	0.8	1.2	0.8
Absolute minimum temperature (ºC)	-17.0 – -7.1	-10.0	-10.1	1.6	-9.8	2.0
Average tree height (m)	6.2 – 17.0	11.7	12.6	2.8	10.8	3.0
Density of medium sized oaks (trunks 10-30 cm dbh in 0.2 ha)	28 – 450	134.8	170.1	138.5	99.0	50.9
Density of large sized oaks (trunks > 30 cm dbh in 0.2 ha)	0 – 31	5.7	5.0	5.2	7.0	7.9

species potentially attracted to feeders, the garden dormouse (*Eliomys quercinus*) hibernates during winter in this region, and squirrels were never seen in the study oak forests during the sampling period (red squirrel, *Sciurus vulgaris*, is a coniferous specialist in our study area, and no squirrel nest was seen in the surroundings of the census plots).

It was not possible to obtain accurate measures of predation risk in our landscape-scale experiment due to logistic difficulties and the scarcity of the potential predator of the focal species (sparrowhawk, *Accipiter nisus*, Perrins 1998). In fact, no Sparrowhawk was observed during the ca. 110 h of time devoted to fieldwork. Nevertheless, food supplemented and control oakwood plots were interspersed within the same forest tracts, and thus our sampling design is not flawed by potential differences in predation risk among study plots.

Bird censuses and habitat structure

Bird censuses were made by means of 10 min point counts (Bibby et al. 2000), within the first 3 h of the morning and the last 2 h of the afternoon. Censuses were carried out from the 1st of December 2009 to the 31st of January 2010. The settlement period prior to the point count starting was 5 min. All auditory and visual contacts were recorded. Each census plot was surveyed three times throughout the study period. Time elapsed between two consecutive censuses of the same plot was 10-20 days. Average census dates were nearly identical for the 40 woodland plots, and the time span of censuses completely overlapped. Censuses were conducted by the same observers (LMC and JS) on nearly windless (wind speed < 3 $m \cdot s^{-1}$) and rainless days. We estimated bird densities (i.e., birds / 1 ha) correcting for the detectability of the species, by recording the distances to the birds and using DISTANCE 6.0 software (Thomas et al. 2009; see a detailed description of the DISTANCE

sampling approach in Buckland et al. 2001). For calculating the detection model, the detection distances were right-truncated, excluding those farther than 75 m from the observer, thus excluding outliers as recommended by Buckland et al. (2001).

Two adjacent 25-m-radius plots were placed within each census plot to sample vegetation structure (one oriented to the north and the other to the south of the census plot center at distances of 25 m). Measurements defining vegetation structure were average height of oaks, and number of tree trunks within two diameter classes: 10-30 cm and more than 30 cm at breast level. Vegetation structure variables were visually estimated, after previous training, by JS and LMC. Both observers estimated vegetation structure in all plots, and their measurements were averaged for each plot. These habitat variables were selected according to general habitat preferences and foraging substrata (Carrascal and Díaz 2006) of the study species (see the Table 1 for average figures and variation of habitat structure variables), and because they are relevant or species dependent on highly transient vegetation structures associated with the early pre-canopy closure stages of forest growth (Hinsley et al. 2009).

Artificial feeders

Artificial feeders were used to control the effect of food availability experimentally on abundance of oakwood birds. They provided *ad libitum* a highly energetic food resource (peeled raw peanuts). Feeders were metallic cylinders (internal dimensions: 25x5 cm) built with a 4.8 mm mesh net allowing birds access to food. Feeders were located in the centre of the census plots at a constant height of 4 m above ground ($\pm$0.3 m), hung on branches in contact with the trunk by means of special hooks of the same size (30 cm). There was enough variation in tree height and size within each study plot such as to be able to choose suitable branches according to our design. This homogeneous setup of feeders in study plots was chosen in order to minimize the influence of within habitat location of feeders on perceived predation risk, according to distances to trunk, ground, and to the nearest protective cover or the lower edge of tree canopy (see Carrascal and Alonso 2006 for more details on the relationship between the selection of feeding locations within habitat and predation risk, and Turcotte and Desrochers 2003 for landscape-dependent response to predation risk by forest birds in winter).

Artificial feeders were settled in the 20 study plots from 25th November-2009 to 31st January-2010 (average weight: 368 g, SD = 14.6). Feeders remained in the supplemented plots every day of the study period and were replaced before depletion. Two feeders were available for each study plot, such that when one was removed for weighing the other was immediately put in its place.

In order to obtain an accurate consumption rate of supplemented food by birds, the weight loss of feeders was measured. Feeders were dried (40ºC for 48 h) and weighed immediately after (precision 0.01 g) before placing them in the field. At the end of the study periods the final weight of feeders was measured after drying them using the same protocol. The weight loss of each feeder was obtained through the difference between the dry weight of the feeder at the beginning and the end of each period. The amount of peanuts consumed in each period was standardized dividing by the time the feeders had been exposed to birds (expressed in grams of peanuts consumed per daytime hour). Weight loss of artificial feeders should accurately reflect the animal demands on food, as the time the bird community spends using feeders is highly correlated with their consumption rate (r = 0.92 in Carrascal and Alonso 2006 using the same protocol and the same species). Weight loss of feeders between 26th December-2009 and 31st January-2010 was considered as a direct measurement of feeder use by the study species, after birds had had one month's experience with artificial feeders in the experimental oakwood plots. Consumption

rates in the first baiting period (25th November-2009 to 26th December-2009) and in the final study period were highly correlated (r = 0.792, n = 20, P < 0.001). Nevertheless, consumption rate was considerably higher in the final (average = 0.83 g·h^{-1}) than in the baiting (0.25 g·h^{-1}) period (paired t-test, t = 4.44, P < 0.001).

Air temperatures

To describe local winter air temperatures, one temperature logger (Onset HOBO Pendant, accuracy 0.47ºC) was set in each oakwood plot. Loggers were placed on thick trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every ten minutes from 1st December to 31st January of winter 2009-2010. For each recording day (144 measurements), average temperature, average daytime temperature and average night temperature were obtained. The absolute maximum temperature registered was 20.1 ºC (in only one census plot for less than three hours in one day). Temperatures for the 62 days of the study period were averaged for each oakwood plot (see Table 1). These three temperature measurements were highly correlated across days and oakwood plots (r > 0.8). Thus, the average night temperature was selected as a measurement of the thermal state of the environment more probably constraining bird distribution and abundance, considering its clear functional meaning related to maximum thermoregulatory costs at night, and the long duration of winter nights (average duration of night : day during the study period = 14.4 h : 9.6 h). We also considered average daytime temperature less discerning because birds compensate thermoregulatory costs associated with daytime temperature by means of heat production resulting from locomotor muscles during foraging activity (e.g. Cooper and Sonsthagen 2007).

Data analyses

Our study focuses on habitat use and food consumption by a defined guild of species, and not on inter-individual differences in patterns of habitat use, so the proper sample unit is the woodland plot. Relationships between bird density (birds·ha^{-1}) or food consumption rate (g·h^{-1}), and the potential explanatory variables were explored by means of generalized linear regression models (canonical distribution: normal; link function: logarithm), using the information–theoretic model comparison approach (food supplementation was included as a dummy variable: not-supplemented = 0; supplemented = 1). Several alternative models were compared with Akaike's second-order AIC corrected for small sample sizes (AICc; Burnham and Anderson 2002) to assess their weights of evidence. For the analysis of bird density per oakwood plot, these models included exclusive effects of habitat characteristics (altitude and vegetation structure; HC), night temperature (NT), food supplementation (FS), and the combination of these factors (HC+NT, HC+FS, NT+FS and HC+NT+FS). For the analysis of food consumption rate in supplemented oakwood plots, these models included exclusive effects of habitat characteristics (altitude and vegetation structure; HC), night temperature (NT), bird abundance (BA), and the combination of these factors (HC+NT, HC+BA, NT+BA and HC+NT+BA).

We also carried out AIC multimodel inference using the seven *a priori* models for bird density and food consumption rate. Rather than base inferences on a single, selected best model from an a priori set of models, inference is based on the entire set of models using weights (W_i) derived from AICc figures. This approach has both practical and philosophical advantages, as it is based on the Kullback-Leibler information theory. A model-averaged estimator has a more honest measure of precision and reduced bias compared to the estimator from just the selected best model (Burnham and Anderson 2004). Standardized regression

coefficients (β), and their standard errors (se), were obtained in regression analyses. Parameter estimates (β and se) were averaged using model weights (W_i) derived from all models in which the predictors occurred (see also Crampton et al. 2011 for a similar approach).

For the sake of brevity we only present the results for the total bird density of the study species; very similar results are obtained when analyzing data singly for the Nuthatch, Great and Blue Tit. Therefore, and for the sake of brevity, we avoid the presentation of results for each species.

The residuals of the two regression models did not show a clear spatial autocorrelation pattern (tested by means of a two-order polynomial of latitude and longitude; Legendre 1993): P = 0.31 for number of birds per plot, and P = 0.59 for food consumption rate. Thus, there was a lack of influence of the spatial location and proximity of the 40 oakwood plots on the observed patterns of variation in the response variables.

All the statistical analyses were carried out using Statistica 10.0 (StatSoft Inc, Tulsa, Oklahoma).

Results

Relative abundance of consumers

Average bird density of the study species per census plot was 5.2 birds·ha^{-1}, ranging between 0 and 12.8 birds·ha^{-1} (see Table 1). The Nuthatch and the Blue Tit were the most common and widespread species (more than 1.7 birds·ha^{-1}).

From the seven *a priori* models exploring the among woodland plot variation in bird abundance (Table 2), the model including night temperature and food supplementation was the one with the highest strength of evidence (model weight, W_i = 0.772; R^2 = 0.335). Its weight of evidence was considerable higher than that of the model including only habitat characteristics (W_i = 0.006). The food-supplemented factor and average night temperature were the predictor variables with the highest magnitude effects (weighted averages of β = 0.42 for both variables). Density of large trees was also an important predictor variable, although its magnitude effect was considerably lower (weighted average of β = 0.294). The rest of predictor variables played a minor role determining bird numbers of small passerines exploiting artificial feeders (absolute values for weighted averages of β < 0.17; Table 2). Thus, birds were more abundant in mature oakwoods supplemented with food and with higher average nocturnal temperatures (see Fig. 1 for the partial residual plots of food supplementation and night temperature with the relative abundance of birds after controlling for all other variables).

The interaction between the effects of temperature and resource availability was not significant in determining bird abundance (ANCOVA model testing for the interaction term night temperature x food supplement: $F_{1,36}$ = 0.16, P = 0.69).

Variation in feeder consumption

Two models analyzing the variability in feeder consumption in experimental oakwood plots had similarly high strengths of evidence (ΔAICc < 2; Table 3). They included habitat characteristics and explained more than one half of variance in feeder consumption. The model with the highest strength of evidence (W_i = 0.382) explained 50.2% of variance in winter consumption of supplemented food. The most important predictor of feeder consumption was average oak height (with a negative effect), according to the weighted average of standardized regression coefficients (-0.924; as well as density of mature oaks > 30 cm d.b.h.). Average night temperature negatively influenced feeder consumption (weighted averages of β = -0.538). The remaining variables had considerably lower magnitude effects (weighted averages of β < 0.27; Table

Table 2. Alternative models for the relative abundance of tree-gleaning birds using artificial feeders in oakwoods of Central Spain during winter 2009-2010. AICc: AIC corrected for small sample sizes. **X**: predictor variable included in the model. W_i: model weights. R^2: proportion of variance explained by each model. K= number of effects + intercept. beta (β): weighted averages of standardized regression coefficients considering model weights W_i. se β: unconditional weighted average of standardized regression coefficient. *n* = 40 oakwood plots. Food supplementation (FS): experimental addition of artificial feeders. Habitat characteristics: altitude, tree height (HTREE), and tree density of two dbh categories (NT10-30, NT>30: respectively 10-30, >30 cm dbh).

	AICc	ΔAICc	K	W_i	R^2	ALTITUDE	HTREE	NT10-30	NT>30	NIGHT TEMP	SUPPL-FOOD
***A PRIORI* MODELS**											
TEMPERATURE (T)	71.3	7.1	2	0.022	0.160					**X**	
FOOD SUPPLEMENTATION (FS)	71.1	6.8	2	0.026	0.167						**X**
T + FS	64.3	0.0	3	0.772	0.335					**X**	**X**
HABITAT CHARACTERISTICS (H)	73.9	9.6	5	0.006	0.251	**X**	**X**	**X**	**X**		
H + T	73.2	8.9	6	0.009	0.310	**X**	**X**	**X**	**X**	**X**	
H + FS	69.4	5.1	6	0.059	0.3720	**X**	**X**	**X**	**X**		**X**
H + T + FS	68.3	4.0	7	0.105	0.431	**X**	**X**	**X**	**X**	**X**	**X**
MULTIMODEL INFERENCE											
standardized regression coef. (β)						-0.023	0.029	0.166	0.294	0.421	0.422
se β						0.243	0.229	0.181	0.226	0.141	0.143

Table 3. Alternative models for consumption rate of artificial food in oakwoods of Central Spain during winter 2009-2010. AICc: AIC corrected for small sample sizes. **X**: predictor variable included in the model. W_i: model weights. R^2: proportion of variance explained by each model. K= number of effects + intercept. beta (β): weighted averages of standardized regression coefficients considering model weights W_i. se β: unconditional weighted average of standardized regression coefficient. *n* = 20 oakwood plots with the experimental addition of supplementary food. Bird abundance (BA): average density of tree-gleaning birds per plot. Habitat characteristics: altitude, tree height (HTREE), and tree density of two dbh categories (NT10-30, NT>30: respectively 10-30, >30 cm dbh).

	AICc	ΔAICc	K	W_i	R^2	ALTITUDE	HTREE	NT10-30	NT>30	NIGHT TEMP	BA
***A PRIORI* MODELS**											
TEMPERATURE (T)	32.3	5.1	2	0.030	0.020					**X**	
BIRD ABUNDANCE (BA)	30.8	3.6	2	0.064	0.092						**X**
T + BA	33.3	6.1	3	0.018	0.092					**X**	**X**
HABITAT CHARACTERISTICS (H)	27.2	0.0	5	0.382	0.502	**X**	**X**	**X**	**X**		
H + T	27.8	0.6	6	0.282	0.572	**X**	**X**	**X**	**X**	**X**	
H + BA	29.6	2.4	6	0.116	0.532	**X**	**X**	**X**	**X**		**X**
H + T + BA	29.7	2.5	7	0.109	0.618	**X**	**X**	**X**	**X**	**X**	**X**
MULTIMODEL INFERENCE											
standardized regression coef. (β)						-0.261	-0.924	-0.249	0.556	-0.538	0.256
se β						0.355	0.274	0.245	0.501	0.456	0.221

3). Feeder consumption decreased with the development in height of the tree layer and the increase of night temperature (Fig. 2).

Discussion

Our results show the prominent role of the energy-related factors, over habitat structure, in determining bird occupancy and abundance in woodlands during the non-breeding season (see also Crampton et al. 2011). They also show that both components of energy constraints (metabolic costs of residency and food availability) are involved at local scales in the distribution of this tree-gleaning guild of small passerines wintering in Mediterranean montane forests. The positive relationship between bird abundance and night temperature found in our study suggests that winter temperatures play an important role on the spatial distribution and the relative abundance of small passerines (i.e., winter habitat selection that implies local movements towards suitable habitats) even in the seemingly milder Mediterranean montane forests.

Temperature has shown an increasing trend in Spain in the last 25 years (de Castro et al. 2005), consistent with the global increase in mean surface air temperatures detected in the mid- and high-latitudinal continental regions of the northern hemisphere since 1976 (IPCC 2001). This increase has led to important changes in the onset of breeding, clutch size and hatching and fledging success in Mediterranean montane populations of several passerine species (Sanz *et al.* 2003, Potti 2009). Nevertheless, little is known about the influence of temperature on winter bird biology in this region (Senar and Borras 2004). If survival of small birds is particularly sensitive to the combination of low temperatures and food shortage in winter (Newton 1998), then an increase in temperature could play a prominent role in those populations inhabiting cold areas-habitats, such as forests in montane areas or northern latitudes (e.g. Butler et al. 2007, Gregory et al. 2007). Our results are consistent with these expectations, as the short term variation of bird abundance is tightly correlated with nocturnal winter temperature. Moreover, there have been marked general increases of these species in the last decade in the same region of cold Mediterranean climate (northern Madrid province; Palomino et al. 2006; significant yearly population growth rates for Nuthatch 11.6%, Great Tit 4.8% and Blue Tit 8.6%). This effect may be acting despite the fact that fewer young usually fledge with warmer temperatures (see Potti 2009 for the study

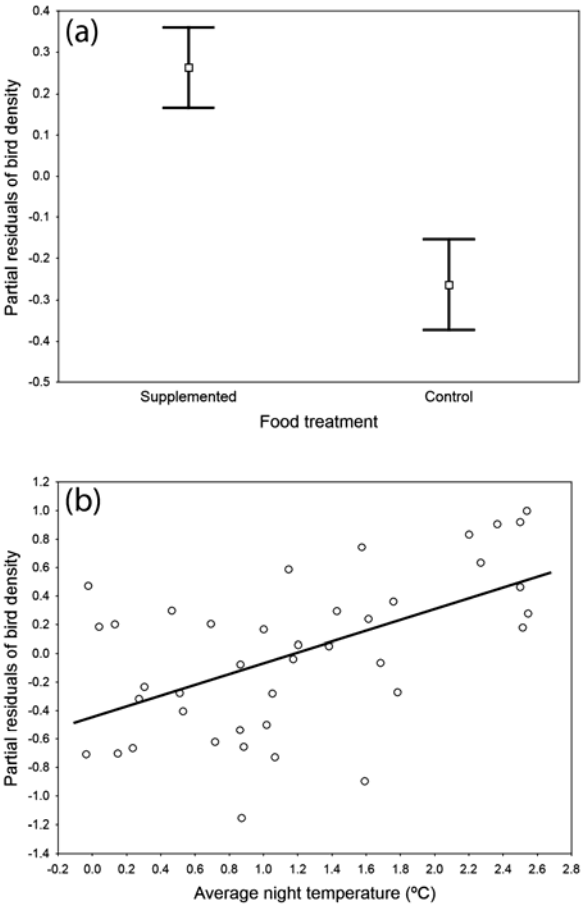

Figure 1. Partial residual plots illustrating the influence of food treatment (a) and average night temperature (b) on the relative abundance of tree-gleaning birds using artificial feeders in oakwoods of Central Spain during winter 2009-2010. n = 40 oakwood plots (20 oakwoods with the experimental addition of artificial feeders, and 20 not supplemented). Partial residuals are obtained after controlling for the remaining variables considered in the analysis of Table 2. Vertical bars show mean±standard error.

region). Recently, Cresswell et al. (2009) have shown that the increase of 6.5ºC from 1995 to 2005 in mean daily winter temperature decreased the starvation risk of Great Tits in England (birds responded to this scenario by decreasing their body mass). Therefore, global warming may exert a positive influence in woodland temperate avifaunas, favouring winter residency and enhancing winter survival, thus translating into positive population trends on a regional basis.

By means of a food supplementation experiment over a large extension of homogeneous forests, our results demonstrate that bird abundance of the studied tree-gleaning guild was significantly higher in the presence of the artificial feeders, after controlling for local differences in habitat structure and temperature. The great importance of food availability on north European wintering populations has been also found at southern latitudes with less stressful winter conditions (Pérez-Tris and Tellería 2002, Guitián and Munilla 2008, Tellería et al. 2008). Nevertheless, food limitation might not be very stringent in these Mediterranean forests of cold climate. Boutin (1990) reviewed the available literature and found that the typical population response to food supplementation was two- to three-fold increase in density in small-bodied animals in north temperate environments. Local abundance of Black-capped Chickadees (*Poecile atricapilla*) wintering in a cold mixed woodland of North America (Maine, average December-January temperatures of -10.4º C; Wilson 2001) was 55-times higher in supplemented than in unsupplemented plots, compared to a 1.7-times increase in our study area (with an average temperature of 2.3º C; see Table 2). Therefore, supplementary food resources in these Mediterranean montane oakwoods may be a solution when foraging conditions suddenly become worse (i.e., cold spells), or to overcome short periods of deficient energy budgets (e.g. early in the morning after a very cold night). In such situations, feeders may play an important role as an abundant and predictable food resource to rapidly meet high energy demands (see Carrascal and Polo 1999 for experimental evidence with the coal tit in the same study region).

Our results support a greater consumption of supplementary food in colder conditions at the regional scale (see also Kwit et al. 2004, Chamberlain et al. 2005, Zuckerberg et al. 2011). Nevertheless, and more interestingly, the relative contribution of a fixed amount of supplemented food to its consumption by birds decreased with vertical development of oakwoods (i.e., oak height; see Fig. 2a), which could be explained considering that taller trees provide more structural resources available to foraging and therefore increase absolute natural food

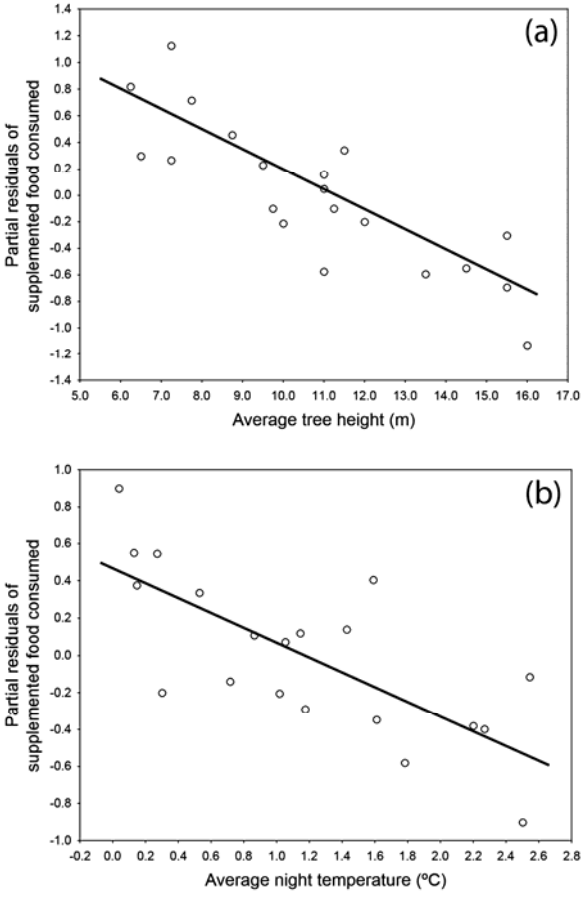

Figure 2. Partial residual plots illustrating the influence of average tree height (a) and average night temperature (b) on the consumption rate of artificial feeders in 20 oakwood plots of Central Spain during winter 2009-2010. Partial residuals are obtained after controlling for the remaining variables considered in the analysis of Table 3.

availability per unit area. Chamberlain et al. (2007) have also found that the use of artificial food sources by birds is influenced by resources in the surrounding habitat. Therefore, broad variation in habitat structure at regional scale may weaken the subtle effect of the spatial variation in ambient temperature on consumption of supplemented food (e.g. Turcotte and Desrochers 2005).

The relationship between population density and temperature would be dependent on resources, because individuals adjust their foraging activity to meet the energetic demands of the environments they occupy and bird densities often change in relation to varying food supplies (Newton 1998). Therefore, at low resource levels (control plots) we could expect a tighter relationship between abundance and temperature than at high resource levels (supplemented plots). However, we found that temperature affected abundance independently of resource levels. According to species-energy theory this suggests that our study area in winter is, despite food supplementation, a low-energy scenario where the relationship between biodiversity and energy is predicted positive linear (Phillips et al. 2010). Indeed, average minimum night temperatures were low and within the range of 0.05 to 2.54 ºC (see Fig. 1b), so birds spend a very long proportion of the winter day without foraging and at temperatures approximately 20 ºC below the thermoneutral zone (average night duration: 14.4 h or 60% of a winter day). Moreover, there must be a limit to acclimatization capacity, even in overabundance of food, mainly because there is a limit to the amount of reserve a bird can carry to survive overnight (McNamara and Houston 1990, Witter and Cuthill 1993). In such conditions, temperature would be limiting even if food resources are abundant. Therefore, even under abundant food, birds may have remained limited by ambient temperature. Their limit of cold tolerance could have improved due to food availability, but not to a point where they can physiologically escape from the effects of temperature.

In conclusion, this study highlights the prominent role of the energy-related factors, over habitat structure, in determining the abundance of birds living under constraining wintering conditions. The positive influence of food availability on bird abundance was mediated by vegetation structure, with a lower influence in maturer oakwoods. The positive correlation of abundance of the studied species with nocturnal winter temperature, together with the regional population increases of these species recorded during the last decade, show that an increase in winter temperature due to global warming could play a prominent role in these small birds inhabiting cold Mediterranean areas-habitats.

Acknowledgements

This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Educación y Ciencia. We also thank Will Cresswell for his useful comments on the original manuscript and Claire Jasinski for improving the English of the manuscript.

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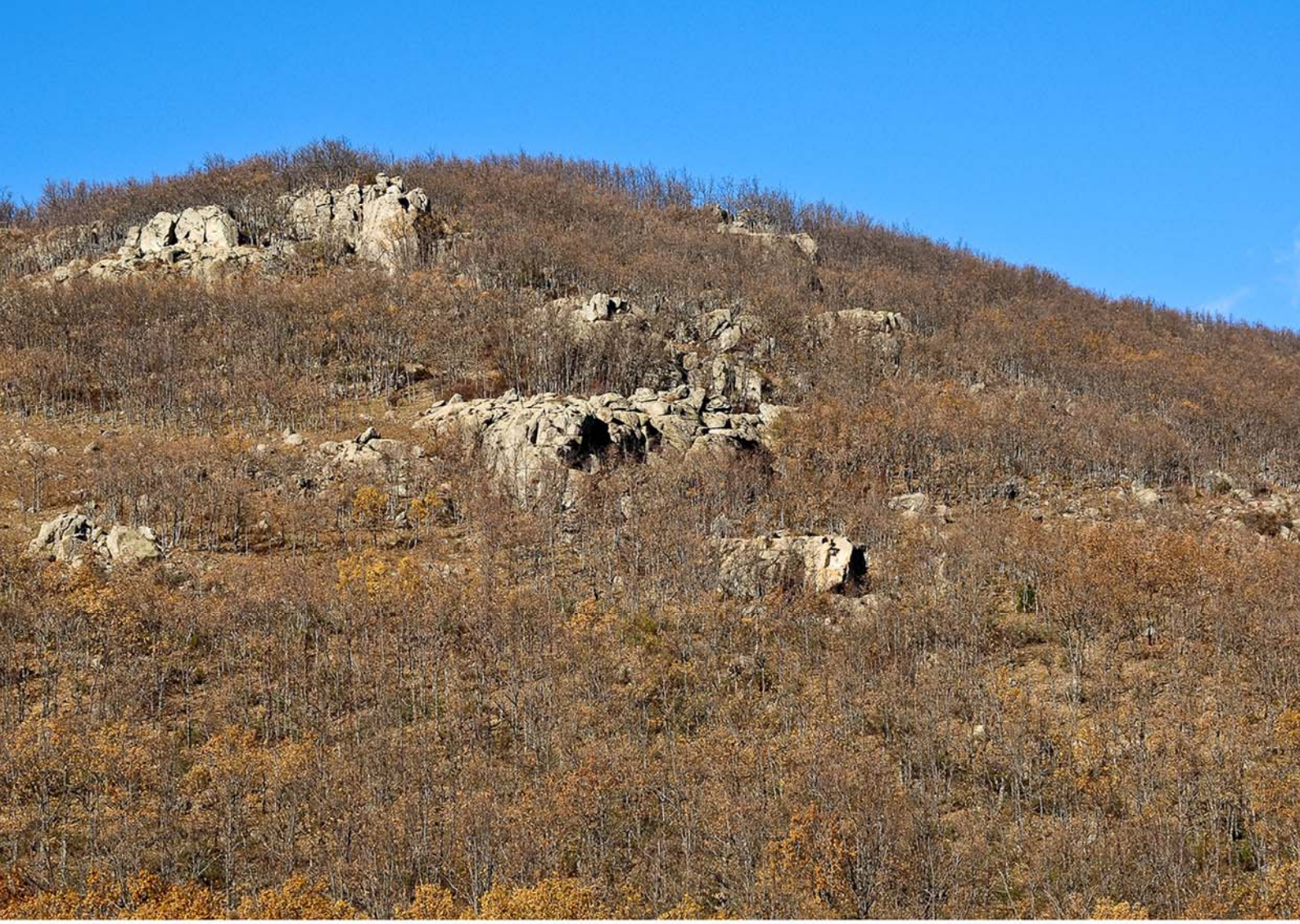
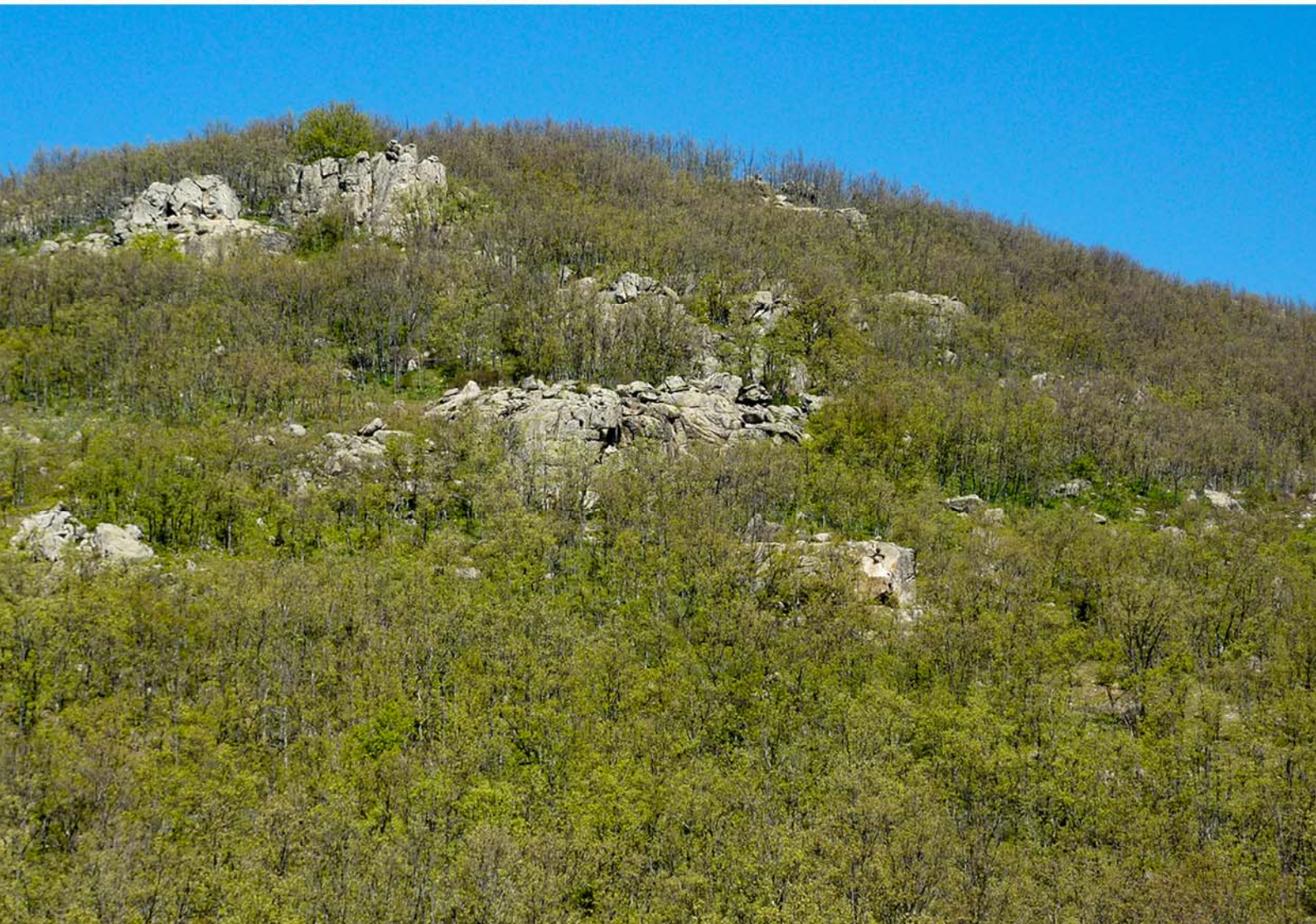
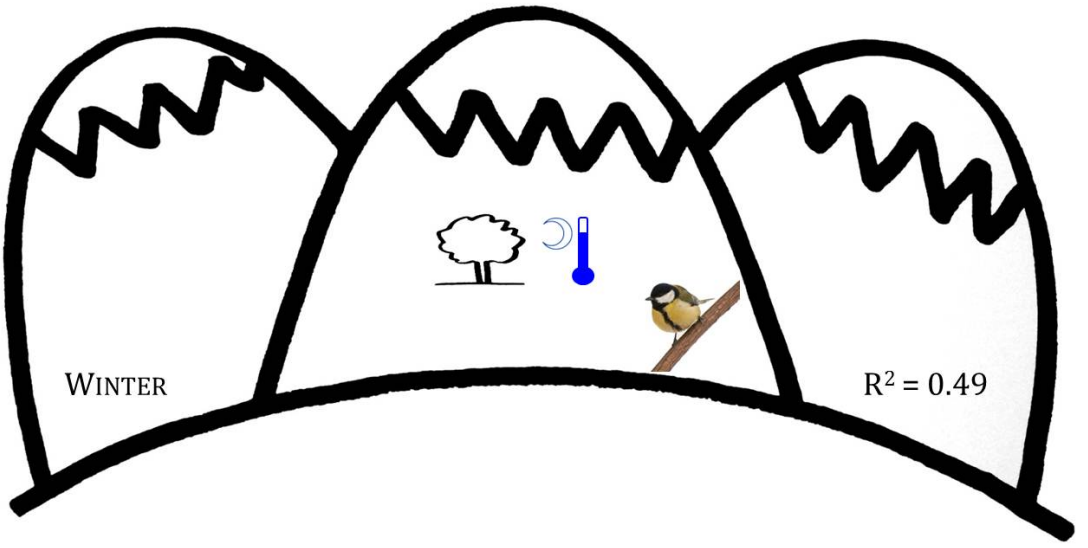




Chapter 6

Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods


WINTER
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SPRING
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Determinantes ambientales de la estacionalidad en la diversidad de aves de robledales mediterráneos

Objetivo Comparar la influencia de factores bióticos (estructura de la vegetación y fenología) y abióticos (temperatura y altitud) determinando la riqueza y el encajamiento de especies de aves en invierno y en primavera.

Localización Robledales montanos mediterráneos de la Sierra de Guadarrama (escala regional).

Métodos Se analiza la riqueza de especies de aves forestales y el encajamiento de las comunidades a lo largo de 40 puntos de muestreo, en invierno y primavera, durante dos años consecutivos. La temperatura se mide de forma local con registradores de temperatura, mientras que la estructura de la vegetación y la fenología del desarrollo foliar se estiman visualmente.

Resultados y discusión La variación espacial en la riqueza y el encajamiento de especies es más determinista en primavera que en invierno. Las aves reproductoras prefieren bosques bajos con temperaturas frías a mediodía (presumiblemente para evitar el estrés por sobrecalentamiento en verano), un clima menos impredecible, y un desarrollo del follaje más temprano. Sin embargo, en el invierno los factores más deterministas son la temperatura nocturna y la madurez del arbolado. Las temperaturas diurna y nocturna tienen efectos radicalmente opuestos en invierno y en primavera.

Conclusión Tanto los factores bióticos como los abióticos afectan a las comunidades de aves locales, pero los componentes específicos varían entre estaciones. Estos resultados realzan la importancia de los estudios a escala fina para contemplar la variación temporal y entender los patrones de biodiversidad regionales, tanto actuales como futuros.

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Seoane J, Villén-Pérez S, Carrascal LM **(2013)** Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods. *Ecological Research* 28: 435-445

Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods

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Abstract The strong season-to-season variation (seasonality) in abiotic factors and productivity shape the changing patterns of species distribution and diversity throughout the year in temperate ecosystems. However, the determinants of seasonal changes within animal communities have rarely been explored, and the prognosis of community variation typically relies on identifying simple factors (e.g., mean temperature) that are assumed to have a constant effect throughout the year. Here we analyze the competing and changing roles of biotic (vegetation structure and phenology) and abiotic (temperature and elevation) factors in determining the richness and nestedness of montane Mediterranean oakwoods (central Spain) bird species in winter and spring. In winter, the most energy-demanding period, birds prefer mature forests with higher nocturnal temperatures where they can minimize thermoregulation costs during the long winter nights. In spring, which is the breeding season, spatial variation of species richness and nestedness is more deterministic than in winter. Breeding birds prefer lower forests with cooler temperatures at midday (presumably to avoid summer overheating stress), less unpredictable weather, and where trees develop leaves earlier (suggesting that birds, particularly those that prey on folivorous insects, would be able to breed early in the season). Thus, although both biotic and abiotic factors take part in the assemblage of local communities, the intervening specific components vary between seasons. For example, temperature —the factor most widely used to forecast future community changes— had opposite effects in winter than in spring. These results highlight the importance of fine-grained scale studies in accounting for temporal variation to understand both current and future regional biodiversity patterns.

Keywords: *Habitat characteristics · Nestedness · Species richness · Temperature · Winter*

Introduction

At northern mid and high latitudes, a strong seasonality in abiotic conditions and productivity imposes widely different ecological scenarios throughout the year on the communities living in them (Breckle 2002). Seasons impose contrasting demands on animal species, which must respond with behavioral and physiological adaptations, including shifting resource use or migration to other geographical areas with tolerable or more adequate conditions (Wagner 1981, Carrascal et al. 1987, Newton 2007, Suárez-Seoane et al. 2008). Although the temporal dimension of biological diversity has not gone unnoticed, changes among temporal periods are rarely addressed (but see Wiens 1989b, Murgui 2007, Loópez de Casenave et al. 2008). These specific responses translate to greater community patterns in accordance with seasonal variation in environmental factors (e.g. Laiolo 2005).

Composition and species richness of avian communities is associated with habitat structure as well as with abiotic factors such

as temperature and precipitation; these are directly related to primary productivity, and have been broadly studied, both at local and regional scales and at different periods of the year (Wiens 1989a, Honkanen et al. 2010). However, these studies have mainly focused on landscape and habitat structure parameters during the breeding period, and barely at all on the winter season. Moreover, there is a general lack of fine-grained studies exploring whether the factors ruling the assemblage of local communities remain the same or change throughout the year (but see Carnicer and Díaz-Delgado 2008, Murgui 2010).

During the breeding season, birds spatially restrict their mating to a central place due to time and energy constraints imposed by incubation and chick rearing duties. Thus, breeding birds show marked habitat preferences in relation to vegetation structure. Specifically, structural complexity of vegetation (tree maturity in forest environments) seems to be the most important attribute determining species richness and diversity at the local scale (Hurlbert 2004, Hinsley et al. 2009). In contrast, during the winter period, when food resources are much scarcer and weather conditions unpredictable, birds adopt a vagabonding lifestyle exploring a greater variety of habitats over larger areas to track the spatiotemporal distribution of food availability (Levey and Stiles 1992, Wiktander et al. 2001). From this perspective, in determining bird distribution at local scales it should be expected that vegetation structure loses importance in winter with respect to the breeding season. Moreover, the ordered gains and losses of species in assemblages, or nestedness (Wright et al. 1998), is hypothesized to decrease in periods of high mobility and relaxed habitat preferences, as is the case during winter time (Murgui 2010).

On the other hand, wintertime air temperatures in temperate zones of the northern hemisphere are below the thermoneutral zone for small birds (usually between 20 and 32 ºC; Calder and King 1974, Kendeigh et al. 1977), and the duration of nighttime is considerably longer than that of daytime (approximately 9 vs. 15 h in central Spain during mid-winter). Under these circumstances, wintering birds might respond to spatial variations in temperature, resulting in higher populations observed in warmer areas (Meehan et al. 2004, Carrascal et al. 2012). In addition, species–energy relationships may arise because high-energy areas support more individuals and these larger populations may buffer species from extinction, thus leading to an increase of species richness (the ‘‘more-individuals hypothesis’’: Hurlbert 2004, Evans et al. 2005). These stressful temperatures do not usually occur in the breeding season, except for sudden frosts and periods of bad weather conditions in early-mid spring that can compromise reproduction success. However, temperatures in the seasonal environments of temperate areas rise from winter minima to high summer temperatures, which can be above the upper critical temperature for small birds (usually above 32–35 ºC; Calder and King 1974, Kendeigh et al. 1977). Therefore, we expect birds to avoid the warmest areas in summer in order to reduce overheating and drought stress, a fact that seems to be supported by recent changes in species and assemblages in response to extreme heat waves (e.g. Visser et al. 1998, Sæther et al. 2003, Jiguet et al. 2011).

Under this seasonal environmental scenario in temperate areas, intra-annual variation is foreseeable given both the extent to which bird diversity patterns are explainable by biotic and abiotic factors and the relative importance of thermal environment and habitat structure for the assemblage of local communities. However, predictions of species richness and distribution, particularly those forecasted under global change by correlative bioclimatic models, typically disregard these seasonal variations. Thus, most prognoses of community change rely on identifying simple, easy-to-measure factors (e.g., average temperature) that are assumed to have constant effects throughout the year (e.g.,

decreasing diversity; Peterson et al. 2002, Araújo et al. 2006, Pompe et al. 2008).

Here, we explore the seasonality of the avifauna of deciduous forests located in the southwestern Mediterranean region (Central Spain). These montane Mediterranean oakwoods are representative of the most southern broadleaf forests in the southwestern Palaearctic Region (Costa et al. 1998), and face dramatic reductions in their extension as a consequence of the predicted climate warming of the coming decades (Sánchez de Dios et al. 2009). Moreover, woodland bird populations in the Iberian Peninsula are peripheral in the geographical domain of the western Palaearctic, because a large number of species have their core distribution areas in central and northeastern Europe, with geographical variation of woodland bird species richness decreasing towards southwestern Europe (Tellería and Santos 1993, Mönkkönen 1994, Tellería and Santos 1994, Mönkkönen and Viro 1997, Carrascal and Díaz 2003). According to the abundant-center hypothesis, abiotic determinants of species distribution are more stringent toward the periphery of a distribution range (see a review and a critique in Sagarin et al. 2006). Thus, controls of biodiversity are expected to stand out in these peripheral areas.

Concretely, we study the montane oakwoods of central Spain, with a continental Mediterranean climate characterized by cold winters and warm summers. The mountainous study area offers a considerable environmental heterogeneity, both in orographic characteristics (elevation and cardinal orientations) and in habitat structure (tree maturity, canopy cover, and development of shrub and herbaceous layers; mainly because these forests have been intensively managed for charcoal and cattle grazing). This strong seasonal contrast in abiotic conditions in a heterogeneous woodland environment provides an excellent opportunity to investigate the competing roles of several factors in determining species richness and community assembly at a local scale. The goals of this study are: (1) to relate species richness to orographic, vegetation structure and thermal characteristics of woodlands describing factors (ambient temperature, habitat diversity) and resources (food availability) for forest bird species; (2) to assess how the relationships change between seasons; and (3) to test if the nestedness of bird assemblages is lower in the winter than in the breeding season, considering the relaxed habitat preferences and higher mobility of birds in winter. We hypothesize that species richness and the ordered composition of bird assemblages (i.e. nestedness) will be more associated with variables that are directly related to the energy budget of birds in the more energetically demanding season (i.e. winter), while the relevance of variables accounting for the onset of breeding, resource use and niche partitioning will stand out during spring. Also, we will briefly discuss the conservation implications of our findings regarding the influence of temperature and vegetation structure on species richness and distribution.

Methods

Study area and period

The study was conducted in the Sierra de Guadarrama region (Madrid province, Central Spain, 40º54’11’’– 40º33’45’’N, 3º46’08’’– 4º10’03’’W), spanning over 500 km2 at elevations ranging from 900 to 1600 m a.s.l. Woodland plots were selected in monospecific forests of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), covering a wide range of variation in forest maturity, elevation and cardinal slope orientations (to account for the amount of incident solar radiation). The climate of the region is continental cold Mediterranean climate, with abundant snowfall and frost in winter (respectively 15 and 49 % of the days in December and January of 2009–2010), and

sporadic snowfall and frost in spring (respectively 6 and 9 % of the days in May 2009–2010; data from three neighboring meteorological stations with an average elevation of 1272 m a.s.l.; Spanish Agencia Estatal de Meteorologı´a. Ministerio de Medio Ambiente, y Medio Rural y Marino). We censused a total of 40 plots of 75 m in diameter in winter (December–January) and spring (May) of two consecutive years (2008–2010), focusing on 20 plots each year.

Bird censuses, habitat structure and temperature

We surveyed birds using point-count stations (Bibby *et al.* 2000) lasting 10 min. The settlement period prior to the point count starting was 5 min. All auditory and visual contacts were recorded, but only those within a 75 m (1.77 ha) radius were used in subsequent analyses, because a large proportion (76%) of the contacts were detected within this census belt. The same trained persons conducted the censuses (LMC and JS) on nearly windless (wind speed < 3 m s^{-1}) and rainless days, within the first 3 h of the morning and in the afternoon beginning 2 h before sunset. We made an effort to improve accuracy in distance estimates, and to reduce inter-observer variability, by training continuously with a laser rangefinder to the cut-off point of 75 m. Plots were separated by at least 300 m to minimize the probability of sampling the same birds more than once, being the nearest oakwood plots separated by steep ridges. Each year, the censuses were repeated in three different days in December and January (wintering season for all species), and in three different days in May (breeding season for all species). Thus, each oakwood plot had an accumulated census time of 30 min per season, which is adequate for bird surveys of woodland birds (Shiu and Lee 2003). Species richness was estimated as the average number of forest bird species per 10 min census in the three visits, per plot and season.

Two adjacent 25-m-radius plots were placed within each oakwood plot to sample vegetation structure, representing the environmental heterogeneity within the census plot. Measurements defining vegetation structure were covers of the tree and shrub layers (distinguishing four bush types: oak regrowth < 2 m in height; thorny, fruit producing, shrubs of genus *Crataegus*, *Rubus*, *Prunus* and *Rosa*; *Cistus* spp macchie shrubs; and *Cytisus* and *Genista* brooms), average height of the shrub and tree layers, number of trunks within three diameter classes: 5-10 cm, 10-30 cm and more than 30 cm at the breast level, average diameter of the 5 thickest oaks, and number of trunks covered by ivy per unit area (see Appendix 1 for more details on habitat structure in the 40 study oakwood plots). All vegetation structure variables were visually estimated, after previous training, by LMC and JS and their measurements were averaged for each plot. In addition to structure, leaf development was estimated in May when bird censuses were carried out, as a control of tree phenology (Appendix 1).

To describe local winter and spring air temperatures, one temperature logger (Onset HOBO Pendant, accuracy 0.47 ºC) was set in each oakwood plot. Loggers were placed on thick trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every ten minutes from 01-December to 31-January and from 15-April to 16-June in both study years. For each recording day (144 measurements), midday temperature and minimum night temperature were obtained. Temperatures for the 62 days of the study period were averaged for each oakwood plot (see Appendix 1). Temperature loggers were also set in the 40 woodland plots during 62 summer days on July to August- 2010, in order to assess how stressful summer temperatures were in the study area.

Finally, variables summarizing geographical position of the census plots (i.e. elevation and cardinal orientation) were obtained from 1:25000 maps of the Servicio Geográfico Nacional de España. The cosine of the cardinal orientation was used as a

description of the northern-southern component of woodland plots (cos 0º = 1, cos 180º = -1), and thus the amount of solar radiation incidence in the study plots.

We controlled for several confounding sampling artefacts and large-scale effects to test contemporary environmental controls on local species richness patterns. First, sampling was done in equal-sized plots within the same habitat type (montane oakwoods), and thus richness estimates are not affected by area inequality (larger areas bias to larger estimates). Additionally, we controlled habitat structure effects on species richness statistically, by including vegetation structure variables in the analyses.

Data analyses

To assess whether the spatial variation in species richness could be attributed to the potential explanatory variables, multiple linear regression models were built with either species richness or nestedness rank of woodland plots as the response variables, using the information–theoretic model comparison approach. Alternative models were compared with Akaike's second-order information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Only those more plausible models with ΔAICc $\leq$2 were selected. Rather than base inferences on a single, selected best model from an a priori set of models, inference was based on the entire set of models using weights (Wi) derived from AICc figures. Such a model-averaged estimator compares favourably in terms of bias and precision with a single estimator that would be extracted from just the best model (Burnham and Anderson 2004). Standardized regression coefficients (β) were obtained in regression analyses as a measure of the sign and magnitude effects of predictor variables (i.e. analyses were carried out with standardized variables, such that their averages are zero and variances are 1). Parameter estimates (β and R^2) were averaged using model weights (Wi) derived from all models with ΔAICc $\leq$2 (Arnold 2010). All the statistical analyses were carried out using STATISTICA 10 (StatSoft Inc, Tulsa, Oklahoma).

Nestedness describes a pattern of orderly impoverishment in species composition by which poor communities are nested subsets of richer communities. These patterns have been attributed to several mechanisms from passive sampling (sites with larger carrying capacities are more likely to accumulate mores species) to selective colonization and extinction according to area and isolation of sites, and environmental filtering according to habitat quality and heterogeneity (see a review in Ulrich *et al.* 2009). In our study, passive sampling was controlled for by the comparison with suitable null models, and nestedness rank could be linked to environmental descriptors compounding habitat quality, whose importance varied between seasons.

Two indexes were calculated to assess assemblage nestedness among the 40 plots on each season: the matrix temperature (T) and the NODF (Nestedness metric based on Overlap and Decreasing Fill), both based on the arrangement of species on a site (rows) by species (columns) matrix (Rodríguez-Gironés and Santamaría 2006; Almeida-Neto et al. 2008). T, which decreases with nestedness, is the most commonly used metric for assessing overall nestedness (Ulrich *et al.* 2009) and we used it here to facilitate informal comparisons. The newer NODF index has better statistical properties and allows for the quantifying of the separate contribution to nestedness of columns (due to incidence of species) and rows (due to composition of sites; Almeida-Neto *et al.* 2007). NODF increases with nestedness. The significance of these results was estimated by comparison with null model communities, which were simulated randomising the original presence/absence matrix. Two different null models that incorporate plausible biological structures were tried: c_0, which randomises rows and columns in a constrained way to

Table 1. Principal components analysis performed with 12 variables defining habitat structure in 40 census plots (factors PC1-PC3 obtained after varimax rotation).

	PC1	PC2	PC3
Average shrub layer height	0.28	**0.78**	-0.10
Cover of thorny, fruit producing, shrubs	**0.89**	-0.18	-0.02
Cover of oak regrowth (< 2 m in height)	-0.14	**0.77**	0.02
Cover of *brooms* (*Genista*, *Cytisus*)	-0.10	**0.72**	-0.13
Cover of *Cistus* shrubs	-0.17	-0.06	**-0.64**
Tree layer cover	0.30	-0.19	**0.83**
Average oak height	**0.58**	0.24	**0.63**
Density of oaks 5-10 cm dbh	-0.39	-0.26	**0.59**
Density of oaks 10-30 cm dbh	-0.42	-0.43	**0.66**
Density of oaks >30 cm dbh	**0.87**	0.17	0.16
Average diameter of the 5 thickest oaks	**0.88**	0.18	0.09
Number of trunks covered by ivy	**0.82**	-0.24	0.06
Eigenvalue	3.88	2.23	2.37
% variance accounted for	0.32	0.19	0.20

In bold type, significant correlations between variables and factors (at $P < 0.001$). For more details on vegetation structure variables see Appendix.

keep column frequencies, and r_1, which maintains site frequencies and uses column marginal frequencies as probabilities (Jonsson 2001; Moore and Swihart 2007). Thus, null model c0 accounts for among-species differences (such as different abundances) so that significant nestedness would be attributed to variation in observed richness, while null model r1 accounts for among-sites differences (such as different carrying capacities) and, partially, for among-species differences, so that significant nestedness would be attributed to variation beyond observed richness or incidence (Moore and Swihart 2007). 100 randomizations of the matrix were used. We related nestedness rank for sites with environmental variables. These ranks were given as the ordinate in the nestedness plots built with the index T, which are calculated as (k-0.5)/n for k = 1…n rows (i.e., the bottom row in the graphs, which is occupied by the more nested site, has a rank of (1-0.5)/40 = 0.0125). Estimates of nestedness were done with several versions of R (R Development Core Team 2011, versions 2.11 and higher) and the specialized functions of package Vegan (Oksanen *et al.* 2011, versions 1.17 and higher).

Vegetation predictor variables were synthesized in three vegetation structure factors by means of a Principal Components Analysis with Varimax rotation (PCA, Table 1). The first component (PC1) defines a gradient of oakwood maturity according to its positive relationship with oak height, diameter, density of thick oaks, and presence of ivy and a dense and diverse layer of thorny, fleshy-fruit producing, shrubs. The second component (PC2) identifies the woodland plots with a well-developed shrub layer dominated by brooms and oak regrowth. Finally, the third component (PC3) is positively related to density and cover of young oaks (<30 cm dbh).

Results

Species richness

Nearly one half of the observed spatial variation in wintering bird species richness (49.4%) was explained by an average model including oakwood maturity (first vegetation PCA axis in Table 1) and minimum night temperature as the most influential variables ($\Sigma W_i > 0.8$ and highest magnitude effects; two models with ΔAICc

Table 2. Alternative models for species richness of birds in 40 oakwood plots of Central Spain in winter and spring of two consecutive years (2008-2010), ordered by the value of the AICc criterion (with small sample correction).

Winter	PC1	TNOCT	TZENIT	ELEVATION	ORIENT	PC2	PC3	LEAF INDEX	R^2 (%)	W_i	AICc
Standardized regression coefficients (β)											
Model 1	0.45	0.36							49.2	0.70	136.3
Model 2	0.44	0.32	0.08						49.7	0.30	138.0
Weighted average β	**0.45**	**0.35**	**0.02**	**0.00**	**0.00**	**0.00**	**0.00**	**---**	**49.4**		
ΣW_i	**1.00**	**1.00**	**0.30**	**0.00**	**0.00**	**0.00**	**0.00**	**---**			
Spring	ELEVATION	PC3	LEAF INDEX	TZENIT	ORIENT	PC1	PC2	TNOCT	R^2 (%)	W_i	AICc
Standardized regression coefficients (β)											
Model 1	-0.72	-0.41	0.30	-0.27	-0.19				64.1	0.22	149.8
Model 2	-0.72	-0.40	0.34	-0.25	-0.20		-0.18		67.2	0.17	150.3
Model 3	-0.61	-0.41	0.34	-0.24					61.6	0.16	150.4
Model 4	-0.47	-0.40	0.30	-0.21		0.25			65.7	0.15	150.6
Model 5	-0.61	-0.41	0.38	-0.23			-0.18		64.4	0.12	151.0
Model 6	-0.39	-0.32	0.28			0.28			62.6	0.10	151.3
Model 7	-0.56	-0.40	0.29	-0.23	-0.12	0.21			66.6	0.09	151.6
Weighted average β	**-0.60**	**-0.40**	**0.32**	**-0.22**	**-0.08**	**0.08**	**-0.05**	**0.00**	**64.5**		
ΣW_i	**1.00**	**1.00**	**1.00**	**0.90**	**0.47**	**0.33**	**0.29**	**0.00**			

Only those models with an increase in the AICc statistic ≤ 2 are shown. Figures for each variable are beta regression coefficients obtained in general linear models. ΣW_i: sum of weights of the models in which the variable appears; R^2: variance explained by each model (in %); W_i: model weight; PC1, PC2 and PC3 are habitat structure components (see **Table 1**); TNOCT: average minimum nocturnal temperature; TZENIT: average midday temperature; ORIENT: cosine of the cardinal orientation of each woodland plot defining a north (positive) to south (negative) vector; LEAF INDEX: average oak leaf development on 2nd fortnight of May (not possible to analyze in winter time due to the lack of foliage in that season). All models are highly significant ($p<0.001$) using the classical frequentist approach.

Table 3. Alternative models for nestedness rank of bird composition in 40 oakwood plots of Central Spain in winter and spring of two consecutive years (2008-2010), ordered by the value of the AICc criterion (AIC with small sample correction).

Winter	PC1	TZENIT	TNOCT	ORIENT	ELEVATION	PC2	PC3	LEAF INDEX	R2 (%)	W_i	AICc
Standardized regression coefficients (β)											
Model 1	-0.25	-0.25	-0.35						46.2	0.26	1.15
Model 2	-0.27		-0.46						41.8	0.21	1.58
Model 3	-0.39	-0.38							38.6	0.16	2.16
Model 4	-0.36	-0.44		-0.19					41.8	0.15	2.28
Model 5		-0.27	-0.47						41.5	0.13	2.52
Model 6	-0.26	-0.29	-0.31	-0.10					47.0	0.10	2.96
Weighted average β	**-0.26**	**-0.25**	**-0.28**	**-0.04**	**0.00**	**0.00**	**0.00**	**---**	**42.9**		
ΣW_i	**0.87**	**0.79**	**0.70**	**0.25**	**0.00**	**0.00**	**0.00**	**---**			

Spring	ELEVATION	PC1	PC2	PC3	TZENIT	LEAF INDEX	TNOCT	ORIENT	R2 (%)	W_i	AICc
Standardized regression coefficients (β)											
Model 1	0.39	-0.24	0.16	0.25					41.5	0.41	3.19
Model 2	0.42	-0.22	0.17						35.1	0.25	4.15
Model 3	0.45	-0.22	0.15	0.31	0.15				43.0	0.18	4.79
Model 4	0.36	-0.20	0.22	0.27		-0.22			45.6	0.15	5.16
Weighted average β	**0.41**	**-0.23**	**0.17**	**0.20**	**0.03**	**-0.03**	**0.00**	**0.00**	**40.8**		
ΣWi	**1.00**	**1.00**	**1.00**	**0.75**	**0.18**	**0.15**	**0.00**	**0.00**			

Only those models with an increase in the AICc statistic ≤ 2 are shown. Figures for each variable are beta regression coefficients obtained in general linear models. ΣW_i: sum of weights of the models in which the variable appears; R^2: variance explained by each model (in %); W_i: model weight; PC1, PC2 and PC3 are habitat structure components (see **Table 1**); TNOCT: average minimum nocturnal temperature; TZENIT: average midday temperature; ORIENT: cosine of the cardinal orientation of each woodland plot defining a north (positive) to south (negative) vector; LEAF INDEX: average oak leaf development on 2nd fortnight of May (not possible to analyze in winter time due to the lack of foliage in that season). All models are highly significant ($p<0.001$) using the classical frequentist approach.

≤2; Table 2). Winter species richness increased in parallel to minimum night temperature and oakwood maturity (Fig. 1).

Spatial variation in species richness during the breeding season was explained to a greater degree (model average of 64.5% of variance) by the eight predictor variables (seven models with ΔAICc ≤2; Table 2). The variables most affecting spring species richness (ΣW_i >0.8) were elevation (with the highest magnitude effect -*β*-), density and cover of young oaks (PC3 in Table 1), development of oak leaves and average temperature at midday: species richness decreased with increasing elevation, midday temperature and density of young oaks, and increased with advanced development of oak leaves the second fortnight of May (Fig. 2). Cardinal orientation of oakwoods (lower species richness at northern slopes), oakwood maturity (positive effect, first vegetation PCA axis in Table 1) and development of dense shrub layer of oak undergrowth (negative influence) had a marginal role in determining bird species richness during the breeding season.

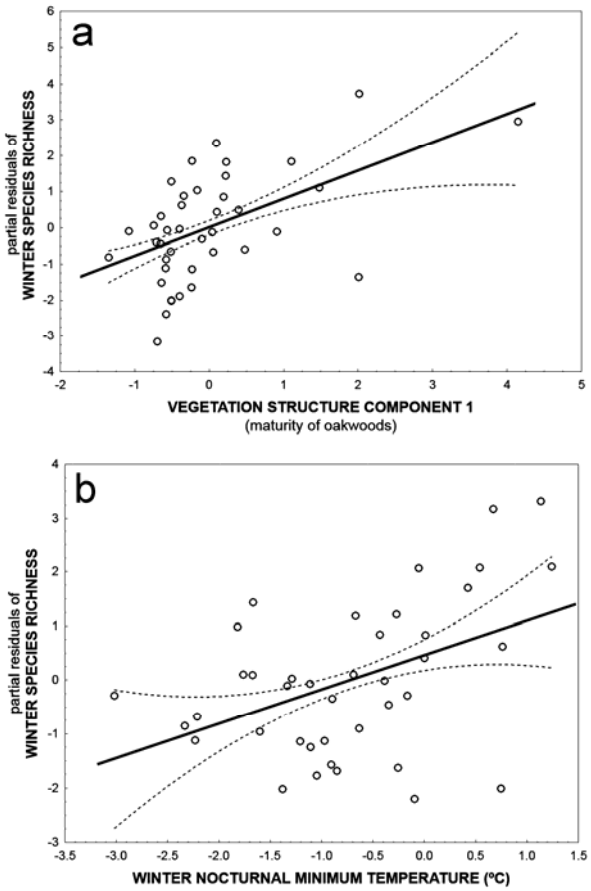

Figure 1. Partial residual plots illustrating the influence of oakwood maturity (a) and winter nocturnal minimum temperature (b) on winter species richness in 40 oakwood plots of Central Spain in two consecutive winters (2008-2010). Residuals are calculated by keeping the other predictor variables except oakwood maturity and minimum temperature, respectively, at their means, thus partialling out their effects.

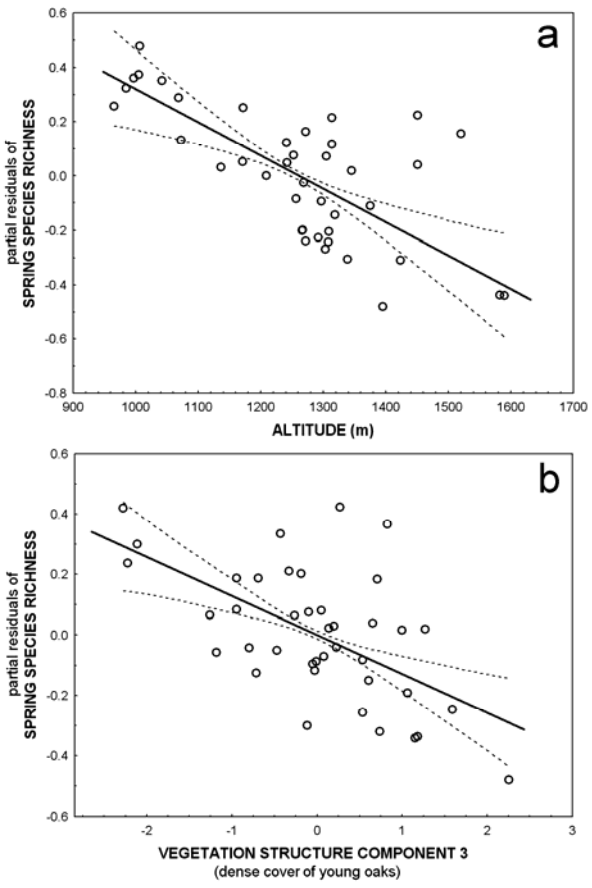

Figure 2. Partial residual plots illustrating the influence of elevation (a) and the dense cover of young oaks (b) on spring species richness in 40 oakwood plots of Central Spain in two consecutive years (2009-2010). Residuals are calculated by keeping the other predictor variables except elevation and cover of young oaks, respectively, at their means, thus partialling out their effects.

There were marked changes in the influence of predictor variables between seasons, as shown by evidence ratios (quotient of variables weights in models of Table 2; we focus here on evidence ratios >7 in variables with weights >0.33 at either season). Average night minimum temperature (positively) was only influential during winter, while elevation and northern cardinal orientation (both negatively) were only influential during spring. In addition, cover of young oaks (negatively) was very influential during the breeding season and had a null effect in winter. Although less clearly related to richness, midday temperature had opposite effects in winter (positive) than in spring (negative).

Nestedness

Both winter and spring assemblages were moderately but significantly nested. Winter assemblages (with a matrix fill of 0.26) had T = 17.8 (P_{r1} = 0.049, P_{c0} = 0.001) and NODF = 58.1 (P_{r1} = 0.001, P_{c0} = 0.001). The contribution of woodland plots (rows) to NODF was larger than the contribution of species (columns; 66 vs 51). Spring assemblages (with a matrix fill of 0.33) had a higher T = 31.4 (P_{r1} = 0.001, P_{c0} = 0.123) and almost the same NODF = 58.9 (P_{r1} = 0.001, P_{c0} = 0.041), which suggests a less ordered matrix (i.e. less nested). Again, the contribution of woodland plots (rows) to NODF was larger than that of species (columns; 61 vs 51). Matrix size and fill were moderate, which means that T estimates are less prone to type-I error (Ulrich and Gotelli 2007).

Nestedness patterns could be attributed to the analysed explanatory variables (see Akaike multimodel inference in Table 3). In winter assemblages, the predictors explained an average of 43% of the variation in nestedness rank (six models with ΔAICc $\leq$ 2). Larger contributions were made by temperature (both midday and minimum night temperatures) and the first vegetation PCA axis (oakwood maturity), all with a negative effect on the nestedness rank. Therefore, colder and younger woodland plots in winter showed an orderly impoverishment in species composition. In spring assemblages, a similar average proportion of the variation in nestedness rank was explained by the descriptors (40%; four models with ΔAICc $\leq$2; Table 3). In this case, larger contributions were made by elevation (with a positive effect on nestedness rank), oakwood maturity (PC1, with negative effect), the development of a dense shrub layer of brooms and oak regrowth (PC2), and the cover of a dense layer of young oaks (PC3; the last two factors with a positive effect on nestedness rank). Thus, communities in spring displayed a gradually impoverishment in young forests with a dense shrub layer located at high elevations.

The most remarkable differences between seasons in the influence of environmental predictors on the orderly impoverishment in species composition of bird assemblages were the high importance of elevation in spring and its null influence during winter, the higher influence of temperature in winter compared to spring, and the higher importance of all vegetation structure components in spring compared to winter (compare Akaike weights in Table 3 between both seasons).

Discussion

Spatial variation in bird species richness of these montane Mediterranean forests is a deterministic phenomenon both in winter and spring. Our results support that patterns of biodiversity can be explained successfully at a fine-grained scale not only by habitat structure variables, but also by abiotic factors summarizing the thermal environment, which are more frequently linked to larger scales (Honkanen *et al.* 2010; Jiménez-Valverde *et al.* 2011). We hypothesized that habitat structure would be the prominent factor defining habitat preferences during the breeding season (Wiens 1989a), while temperature would be prominent in winter because it affects

individual energetics through the increased physiological costs of low winter temperatures, and such constraint predominates over other biotic processes that might also influence distributions (Meehan et al. 2004; Evans et al. 2006). We indeed found that determinants of fine-grained patterns of bird species richness and nestedness of bird assemblages in the studied oakwoods were very different between seasons. This disparity highlights the importance of understanding the mechanisms underlying specific spatial and temporal scenarios when interpreting biodiversity patterns. Moreover, the explained variance in the variation of species richness turned out to be lower in winter (49.4%) than in spring (64.5%). The harsh winter environmental conditions, together with the vagabonding life style of birds during this period directed to confront low resource availability, cold spells and sudden periods of bad weather conditions (Fretwell 1972), should cause species richness to be less deterministic in winter.

Spring and winter assemblages are moderately but significantly nested, with higher nestedness of bird communities in winter than in spring. Murgui (2010) and Fernández-Juricic (2000) studied Spanish urban parks and also found a nested pattern in bird communities during the breeding season. However, in contrast to our results on natural montane forests, which show more marked seasonal changes and where winter is harsher, Murgui (2010) found no nestedness in wintering communities of coastal parks. In that study, some species moved from parks to forage and find refuge in the surrounding urban matrix, a strategy that contributed to the nested pattern but that was not available for birds living in natural forests

Nestedness was weaker for species than for sites, so it is more likely due to site properties (environmental conditions, habitat quality, habitat nestedness) than to species characteristics (local abundances or mass effect; Calmé and Desrochers 1999; Hylander et al. 2005; Almeida-Neto et al. 2008). These results are in agreement with the nested habitat quality hypothesis, which states that gradients of environmental harshness are a cause of nested subset patterns in communities because of differences in tolerance to the deficiency of a resource or condition among the species (Hylander *et al.* 2005). On the other hand, nestedness may additionally be promoted by some specialized species or guilds whose abundances are tightly related to habitat structure gradients, such as trunk foragers that are more dense in mature oakwoods and rare or absent in younger stands (see: Carrascal and Díaz 2006; Roberge and Angelstam 2006; Caprio et al. 2009; for deciduous managed forests in Europe). Therefore, our results show that seasonality influence patterns of ordered gains and losses of species in bird assemblages where environmental characteristics are of higher importance than those related to particular species.

Air temperature has an opposite effect in structuring oakwood bird diversity in winter and in spring. Minimum night temperature has an important positive effect in winter species richness and in the orderly enrichment of winter communities, while having a null effect in spring (Tables 2 and 3). This might reflect the energetic constraints suffered by birds during long winter nights (14 h 41' on 01-January in the study area), when environmental temperatures fall well outside the thermoneutral range for small passerines (usually between 20 and 32 ºC; Calder and King 1974; Kendeigh et al. 1977). Under these high thermoregulation costs, a variation of 4.2ºC in night temperature among woodland plots (ranging from -3.0 to 1.2 ºC, Appendix) can make the difference and thus determine winter species richness through residency-area selection. This is not relevant in spring, when the duration of night is shorter (9 h 32' on 15-May in the study area), night temperatures are considerable higher (see Appendix), and thermoregulation costs are consequently reduced.

Contrary to night temperature, midday temperature has an important negative effect

on spring species richness and an almost null effect on winter (Tables 2). The negative effect of midday temperatures in spring may be reflecting future temperature stress at summer time. Spring midday spring temperature during the study period was not stressful (variation of 16.4 to 23.1 ºC among the 40 woodland plots from 15-April to 15-June), while in summer midday temperature was 27.7 ºC (range 24.3 to 31.0 ºC in July and August) and temperature went over 30 ºC an average of 123 h per plot (range of 0.5 to 346.2 h; data obtained during 62 days on July to August-2010). Moreover, summer and spring midday temperatures were highly correlated across the 40 study woodland plots (r = 0.686). Thus, the negative effect of spring midday temperatures could be related to summer residence and the prevention of high temperatures and water stress in the warmest season (Williams and Tieleman 2000; Tieleman and Williams 2002), an in-advance response to summer stress in these forests. There is a great deal of evidence of the influence of the recent increase in ambient temperatures on the breeding biology of many bird species, both at local and large spatial scales (Visser et al. 1998; Sanz 2002; Sæther et al. 2003; Visser 2008). Increasing temperatures have led to important changes in the onset of breeding, clutch size and hatching and fledging success in Mediterranean montane populations of several passerine species inhabiting oakwoods in Central Spain, with mismatches between the timing of peak food supply and nestling demands and fewer young usually fledging with warmer temperatures (Sanz et al. 2003; Potti 2008; Potti 2009). Therefore we postulate an impoverishment of breeding bird communities in these forests if spring and summer temperatures continue to increase in the future (I.P.C.C. 2007; Brunet et al. 2009), especially at lower elevations where higher temperatures and higher current species richness are found.

Elevation is the most important factor governing species richness and nestedness in spring, while having a complete null effect in winter: elevation has a marked negative effect on both species richness and the nested enrichment of communities in spring (see in Tables 2 and 3 the sum of Akaike weights and standardized partial regression coefficients, after controlling for temperature, vegetation structure and orographic factors). Due to its inverse relationship with temperature (the adiabatic lapse rate), and the negative effect of temperature on species richness during the breeding season, we could expect an increase in species richness at higher elevations. Moreover, recent climate warming has been shown to induce upward elevational shifts of the distributional range of several species that track favourable abiotic conditions (Parmesan and Yohe 2003; Sekercioglu et al. 2008; Maggini et al. 2011; but see Archaux 2004; Popy *et al.* 2010). The positive relationship between elevation and species richness at local scale is also predicted considering the general biogeographic pattern observed for birds in the Iberian Peninsula at larger spatial scales: frequency of occurrence of species belonging to the European, Palaearctic and Holarctic biogeographic groups are usually positively associated with elevation (Carrascal and Díaz 2003). This result may respond to a conservative strategy in the breeding season, when parental investment is most at risk. At higher elevations there is increasing climate instability, including cold spells and snowfalls (0 vs. 9 days of frosts and 0 vs. 2.25 days of snowfalls per month in May-2009 and 2010, in lower versus higher meteorological stations; Spanish Agencia Estatal de Meteorología; Ministerio de Medio Ambiente, Medio Rural y Marino; data for four meteorological stations located at 925-1160 and 1532-1894 m a.s.l.). These unpredictable events may compromise incubation and breeding of woodland birds in the mountainous areas by both suddenly decreasing air temperatures and reducing food availability (see Sanz and Moreno 1995 for a food provisioning experiment in a population of *Ficedula hypoleuca* breeding at high elevation in central Spain). Therefore, it seems that the commonly proposed strategy of altitudinal migration to escape from the

global warming effects is not that simple, as birds depend on climatic variables other than temperature (La Sorte and Jetz 2010).

Relationship between vegetation variables (of habitat structure and phenology) and bird community parameters (species richness or nestedness) seems to be stronger in spring than in winter. Moreover, the relative relevance of each habitat structure component depends on the season. In winter, forest maturity is the only relevant component of vegetation structure for bird species richness, and maturity governs the ordered appearance of species throughout these monospecific forests. Forest maturity is also related to nestedness in the breeding season, in concordance with Fernández-Juricic (2000). Nevertheless, young tree cover negatively affects species richness during this season, being the most important factor with regard to vegetation structure. This result highlights the importance of oak regrowth clearance and thinning (the reduction of the high density of young oaks) in young forests, in order to avoid forest monotony and to increase the heterogeneity of the understory layer. These silvicultural practices will allow a higher penetrability of potential breeding birds of Mediterranean forests contributing to the diversification of the avifauna (De la Montaña *et al.* 2006).

Phenology of leaf development has an important influence on bird species richness in the studied oakwoods. Leaf development is tightly related to the reproductive phenology of birds through availability of arthropods (mainly caterpillars) that depend on temporal changes in the amount and quality of foliage (Van Balen 1973; Forkner et al. 2004). The coupling of the maximal peak in food abundance to the peak in chick feeding demands has important consequences for reproductive success of woodland birds (Van Noordwijk et al. 1995; Buse et al. 1999). Our result completely agrees with a number of studies on these species in the Palaearctic Region that have found a tight correlation between an early breeding date and the reproductive success (for instance, see Sanz 1999 for Blue tit, *Cyanistes caeruleus* and Barba *et al.* 1995 for Great tit, *Parus major*). These two points imbricate the mechanism by which oakwoods with an earlier tree leaf development are preferred by birds, showing higher species richness.

In conclusion, determinism and determinants of bird species richness and community species losses along environmental gradients in montane Mediterranean oakwoods highly depends on the season, highlighting the importance of understanding the underlying mechanisms running under specific scenarios whenever interpreting biodiversity patterns. Winter is the season when species richness and community nestedness are less deterministic, the only important factors being forest maturity and minimum night temperature: wintering birds prefer mature forests with higher nocturnal temperatures where they can minimize thermoregulation costs during the most stringent hours. Bird species richness and community nestedness are more deterministic in spring when birds prefer cooler forests at midday, located at lower elevations, with a lower density of a monotonous undergrowth layer of young oaks, and an advanced tree leaf development where reproduction can be initiated earlier. Even in the more energy-favorable period parental investment seems to be threatened by sudden cold spells associated with higher elevations or midday high temperatures both during the breeding season and the summer.

Aknowledgements

This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Educación y Ciencia. We also thank Claire Jasinski for improving the English of the manuscript.

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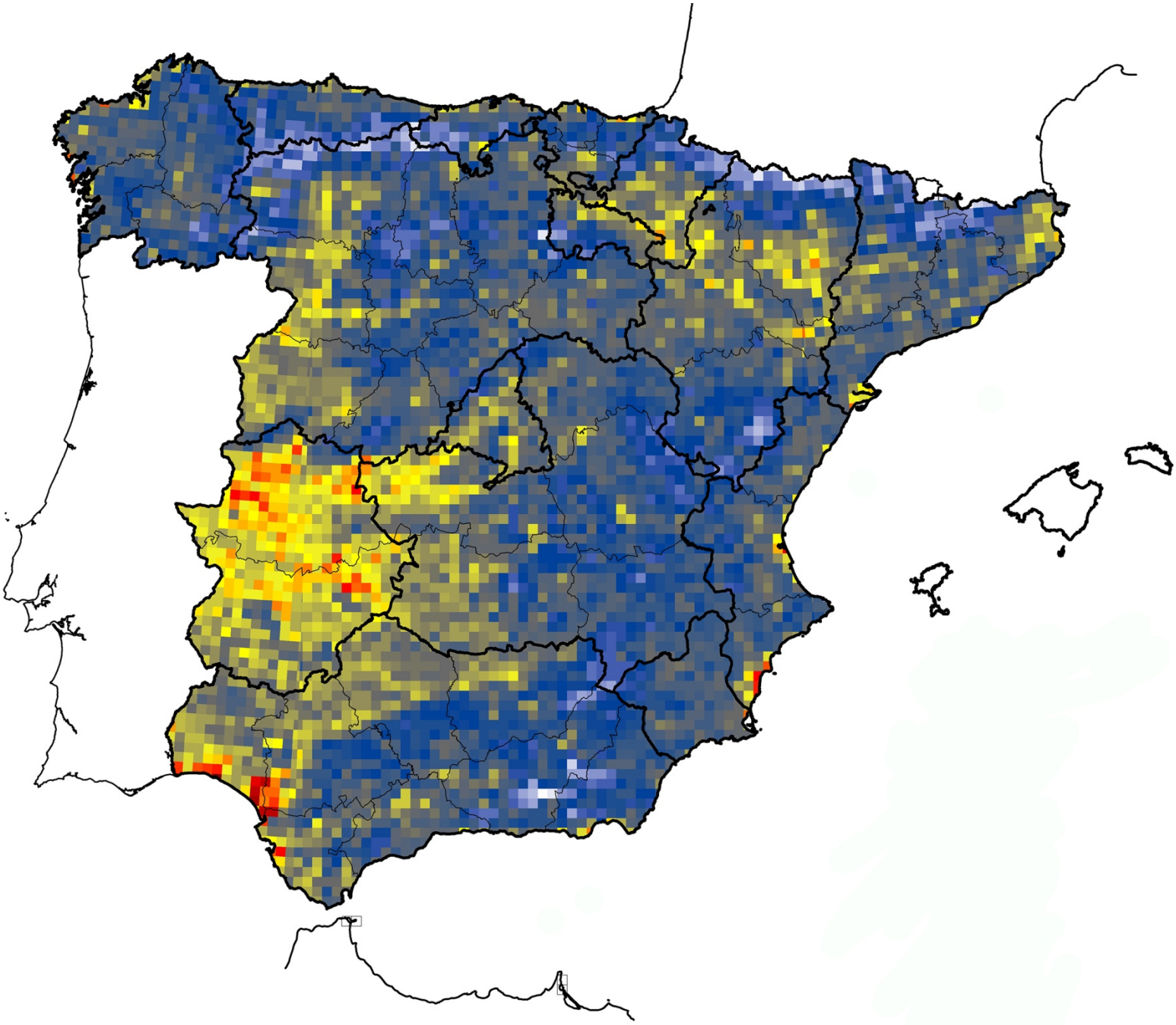
Supporting Information

Appendix. Mean and range of study variables.

Appendix. Mean and range (min / max) of study variables in 40 oakwood plots in Central Spain during winter and spring of two consecutive years (2008-2010).

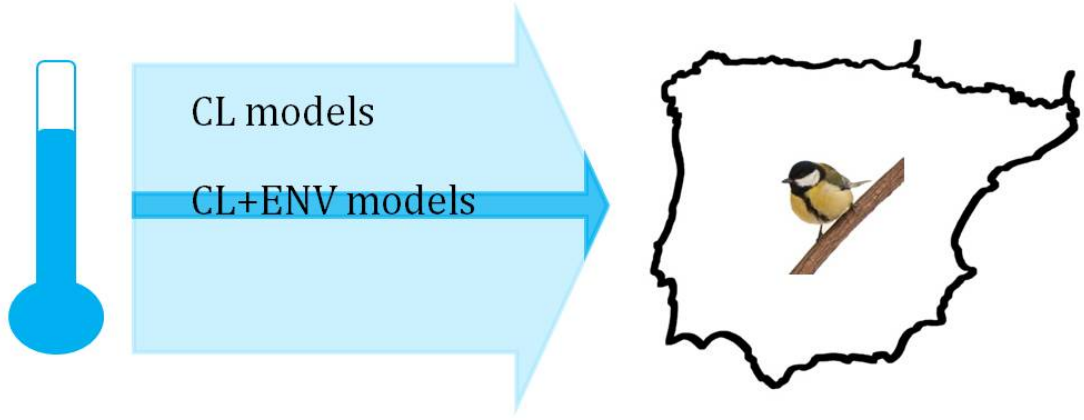
	Mean	Min / Max
Cumulative number of bird species (in 3 censuses); winter	6.6	1 / 15
Cumulative number of bird species (in 3 censuses); spring	12.9	8 / 19
Average number of bird species (in 3 censuses); winter	3.1	0.3 / 8
Average number of bird species (in 3 censuses); spring	8.2	4 / 13.3
Elevation (m)	1260	965 / 1597
Cardinal orientation (º to north)	144	1 / 358
Average air temperature at midday (ºC); winter	5.5	3.4 / 7.1
Average air temperature at midday (ºC); spring	19.9	16.4 / 23.1
Average minimum night temperature (ºC); winter	-0.75	-3.0 / 1.2
Average minimum night temperature (ºC); spring	9.2	6.1 / 11.9
Cover of thorny, fruit producing, shrubs (*Crataegus*, *Rubus*, *Rosa*, …) (%)	4.4	0 / 45
Cover of maquis (*Cistus*) shrubs (%)	3.7	0 / 52
Cover of brooms (*Cytisus* and *Genista* shrubs) (%)	6.4	0 / 37
Cover of oak regrowth (< 2 m in height) (%)	5.3	0 / 50
Average shrub layer height (m)	1.0	0.0 / 2.40
Tree layer cover (%)	64.2	24 / 90
Average oak height (m)	11.7	6 / 17
Density of small sized oaks (trunks 5-10 cm dbh per ha)	508	31 / 2098
Density of medium sized oaks (trunks 10-30 cm dbh per ha)	687	145 / 2292
Density of large sized oaks (trunks > 30 cm dbh per ha)	29	0 / 158
Average diameter of the 5 thickest oaks (cm)	32	19 / 55
Number of trunks covered by ivy (per ha)	22	0 / 357
Oak leaf index (average on 2nd fortnight of May)	4.6	2.3 / 5.7

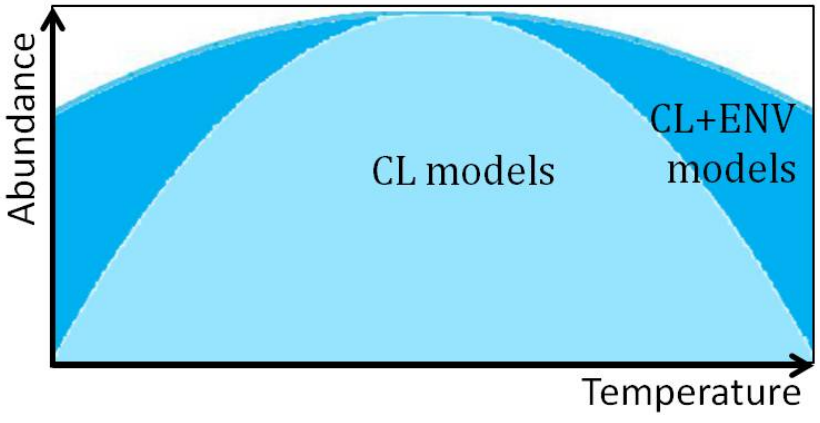
Number of bird species refer to census plots 75 m in diameter.



Chapter 7

Bioclimatic models can provide
misleading projections
when derived only from climatic predictors


CL models
CL+ENV models


Abundance
CL models
CL+ENV
models
Temperature

Los modelos bioclimáticos pueden generar proyecciones engañosas si se basan solo en predictores climáticos

Objetivo (1) Elucidar el efecto de la temperatura sobre la abundancia de aves terrestres invernantes en la Península Ibérica. (2) Analizar la utilidad de los modelos bioclimáticos que solo consideran el clima vs. los que también consideran las preferencias ambientales de las especies.

Localización España peninsular (escala peninsular).

Métodos Modelizamos la variación en la abundancia relativa de 106 especies de aves invernantes a una resolución de 10×10 Km en relación con la temperatura mínima invernal, utilizando regresiones de cuantil al 95% y centrándonos en cuatro parámetros: coeficientes de regresión lineal y cuadrático, temperatura ambiente preferida (a la cual se maximiza la abundancia de las especies), y amplitud térmica (área bajo la curva abundancia-temperatura). Cuantificamos estos parámetros en modelos que solo contemplan la temperatura y la precipitación (CL), y en modelos que además incluyen el uso del suelo, la topografía y la localización espacial (CL+ENV).

Resultados y discusión. En promedio, las aves seleccionan áreas de invernada 2.9ºC más cálidas que la temperatura invernal media en la España peninsular. Además, predominan las relaciones positivas entre la abundancia de las especies y la temperatura. Los modelos solo climáticos tienen un poder explicativo considerablemente menor que los modelos que también incluyen variables ambientales. Las parametrizaciones de los modelos que no consideran variables paisajísticas, topográficas y espaciales están fuertemente sesgadas, y se relacionan débilmente con las de los modelos que sí las consideran. Los modelos solo climáticos sobrestiman la influencia de la temperatura sobre la abundancia de las especies y subestiman la plasticidad de las especies para responder a cambios en la temperatura.

Conclusiones La temperatura es un importante limitante de la distribución de aves invernantes en la Península Ibérica. Sin embargo, debemos considerar las preferencias ambientales de las especies al predecir sus respuestas a la temperatura, tanto en escenarios actuales como de calentamiento global. Si no lo hacemos, corremos el riesgo de generar modelos bioclimáticos fuertemente sesgados con predicciones que podrían inflar la magnitud de los efectos del cambio climático.

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Villén-Pérez S, Carrascal LM, Palomino D. Bioclimatic models can provide misleading projections when derived only from climatic predictors

Bioclimatic models can provide misleading projections when derived only from climatic predictors

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Abstract Aims: (1) To disentangle the effect of minimum winter temperature on the abundance of terrestrial birds wintering in the Iberian Peninsula. (2) To analyze the usefulness of bioclimatic models that only account for climate vs. those that also account for environmental preferences of species. Location: Peninsular Spain. Methods: We model the variation in relative abundance of 106 wintering bird species at 10x10 Km resolution with minimum winter temperature using 95%-quantile regressions and focusing on four parameters: linear and quadratic regression coefficients, environmental preferred temperature (at which the species abundance is maximized) and thermal breadth (area under the abundance-temperature curve). We quantify these parameters for temperature in climatic only (CL) models (temperature + precipitation) and in models also including land cover, topography and spatial location (CL+ENV models). Results: On average, birds actively select to live in areas 2.9 ºC warmer than the average in peninsular Spain, and there is a preponderance of positive relationships between temperature and species abundance. Models with climate only variables have considerably lower explanatory power than models also including environmental variables. Models not accounting for landscape, topographic and spatial patterns of species may incur in strong biases when parameterizing the response of birds to temperature. The regression coefficients for temperature in CL models are loosely associated with those obtained in CL+ENV models. Climatic only models overestimate the influence of temperature on species abundance and underestimate the plasticity of species to respond to temperature changes. Main conclusions: Temperature imposes important restrictions to the winter distribution of birds in the Iberian Peninsula. However, we must control for the environmental preferences of species when predicting their responses to temperature, either under current or future scenarios of global warming. Otherwise, we are at risk of generating strongly biased bioclimatic models that will inflate the magnitude of predicted climate change effects.

Introduction

The distribution of birds that overwinter in temperate ecosystems is assumed to be strongly influenced by environmental temperature, notably in regions with a marked year-round seasonality. Winter is an energy-limiting period in which food resources are scarce and/or difficult to locate, weather conditions are unpredictable (Fretwell, 1972), and the low temperatures impose a high metabolic cost to maintain a constant body temperature for homeothermic animals (Calder & King, 1974). Winter survival depends primarily on a positive energy balance, obtaining enough food for self-maintenance and reducing metabolic costs of thermoregulation (e.g. Newton, 1998). In this ecological scenario, where environmental temperature is well below the thermoneutral zone (ca. 18-22 ºC for a broad variety of species, Calder & King,

1974; Kendeigh et al., 1977), species abundances are expected to be maximal in the warmest areas, through the direct effects of reduced temperature-related mortality and thermoregulation costs, or indirectly via the improvement of the winter foraging environment (e.g., Gosler, 1996; Doherty & Grubb, 2002; Rogers & Reed, 2003; Robinson et al., 2007; Cresswell et al., 2009; Carrascal et al., 2012a). On the other hand, it is highly probable that the response of species abundance or occurrence to temperature also contains the response to other environmental factors directly related to species-specific habitat or trophic preferences, due to the surrogate character of temperature. For example, wintering birds in the southwestern Palearctic clearly show marked preferences for particular habitats with contrasting environmental temperatures (Herrando et al., 2011; SEO/BirdLife, 2012), and small-scale variations in food supply and habitat structure play an important role in wintering populations, of a higher or similar magnitude than temperature (e.g., Pérez-Tris & Tellería, 2002; Guitián & Munilla, 2008; Tellería et al., 2008; Carrascal et al., 2012a). The influence of temperature may also be confounded with related spatial effects, such as the influence of the biogeographical history of species over large-scale distribution patterns (Rahbek et al., 2007), or the importance of day length duration considering time constraints in energy acquisition during winter (Carrascal et al., 2012b). Thus, the influence of temperature on bird distribution and abundance is also probably mediated through surrogate effects of spatial effects, habitat preferences or resource availability (see Aragón et al. 2010 for direct and indirect effects of climatic and non-climatic factors on distribution of ectothermic and endothermic vertebrates in the Iberian Peninsula).

Bioclimatic models are used to assess the potential effects of global warming on species distribution based on the current relationship between species geographical ranges and climate (mainly temperature; Jeschke & Strayer, 2008). This ambitious approach is of interest for predicting environmental impacts of climate change, but makes various controversial assumptions (Pearson & Dawson, 2003; Heikkinen et al., 2006; Araujo & Peterson, 2012), including the omission of relevant predictor variables. Variables that are highly related to current species distribution (e.g., landscape characteristics, habitat structure, food resources availability, biogeographical history; Wiens, 1989; Brown et al., 1996) are omitted in predictive models because it is very difficult, if not impossible, to prognosticate their future changes (e.g., land cover, Rounsevell et al., 2006). However, disregarding these relevant variables may result in 'widely incorrect' predictions (Hampe, 2004), a generalized concern with bioclimatic envelope models (e.g., Pearson & Dawson, 2003; Beale et al., 2008).

Moreover, explanatory environmental variables in distribution models are usually non-independent, which may bias model parameter estimation (Quinn & Keough, 2002). Climatic, spatial, topographic and habitat variables are naturally inter-correlated, and species distribute along multivariate gradients that include strong interactions among variables (e.g., Lobo et al., 2001, 2002; Seoane et al., 2004; Carrascal & Seoane, 2009). When the goal is to infer responses to ecological factors, collinearity among explanatory variables can obscure the emergence of actual environmental / species-specific relationships of true functional meaning. This is of concern when the search for causal patterns is pursued by means of the use of environmental surrogates (e.g., Levin, 1992; Shipley, 1999; Lobo et al., 2002, 2006). For instance, there are synergistic effects between climate change and habitat loss with measurable effects on biological populations (Mantyka-Pringle et al., 2011). This means that the effect of temperature considered alone may in fact reflect the effect of surrogate variables such as altitude or vegetation type. Thus, it is important to know whether ignoring other environmental factors in bioclimatic models can result in a different parameterization of the relationship between

temperature and species occurrence or abundance, or in different position and breadth of species in thermal gradients. This is a key point in understanding the biases assumed when modeling future species distributions with bioclimatic models, and something to consider when evaluating the performance of forecasting models (see also Jeschke & Strayer, 2008). The evaluation of the biases assumed when not controlling the effect of other environmental factors than temperature is better achieved with current accurate data than with uncertain predictions of the future environment that are not truly falsifiable. However, to our knowledge, the quantitative consequences of not considering other environmental factors have been assessed rarely and only for future predictions (Luoto & Heikkinnen, 2008; Sormunen et al., 2011; Triviño et al., 2011; Barbet-Massin et al., 2012). For example, Triviño et al. (2011) found in working with breeding birds of the Iberian Peninsula that models using all predictor variables were not significantly better than models fitted with climate variables alone for ca. 50% of the cases, and that models using climatic variables generally fit the data better than models using vegetation or landscape configuration variables (although they use a restrictive subset of predictors).

Due to the complexity of ecological processes, the relationship between species and temperature needs to be addressed from a functional point of view, with clear functional hypotheses related to specific variables and developed under well-defined spatial and temporal scenarios (Reside et al., 2010; Bateman et al., 2012). Classical correlative and modeling approaches treat species distributions as a 'black box', with the single purpose of describing how species distribute along environmental gradients (Araújo & New, 2007; Rahbeck et al., 2007; Jiménez-Valverde et al., 2011). However, in order to understand how species relate to temperature and how species-specific responses shape the observed global distribution patterns, we need to have more control on how environmental predictors interact with temperature. Here we suggest a way to deepen the association between species' distributions and temperature, using species' abundances, quantile regression and controlling for the effects of several potentially relevant factors in distribution of organisms (precipitation, land cover, habitat diversity, topographic and spatial predictors). By analyzing species abundance through quantile regression analysis (Cade & Noon 2003) the emphasis is put on the areas where temperature is actually limiting abundance over other factors, even taking into account uncertainties in the response variable associated with data quality in extensive sampling. Thus, the limiting influence of temperature is measured at the maximum response of organisms (i.e., maximum ecological abundances; Figure 1a). By means of the use of linear and quadratic terms of temperature, its curvilinear influence can be estimated, allowing us to obtain two important parameters describing the response to thermal gradients: the 'environmental preferred temperature' that maximizes the species' abundance within the thermal span of the study region; and the breadth of the thermal response considering the area under the curve parameterized by the regression coefficients, which represents the plasticity of species in utilizing the thermal space (Figure 1b). These analyses can be carried out considering the partial effect of temperature, either in climate-only models that consider the linear and quadratic terms of temperature and precipitation, or in more complex models where other environmental predictors are included.

The main goal of this paper is to disentangle the effect of minimum winter temperature on the abundance of terrestrial birds wintering in the Iberian Peninsula. We use data from the Atlas of Birds in Winter in Spain (SEO/BirdLife, 2012) for 106 terrestrial bird species quantitatively sampled in 1,689 10x10 km UTM cells, using a standardized protocol of sixty 15-min line transects. This region is an important target for many avian populations of the southwestern Palearctic during the winter

(Moreau, 1972), a period in which temperature drops and there are massive migrations of northern populations towards circum-Mediterranean countries.Temperature might have a more marked influence on bird distribution during winter than in other periods such as the breeding season when temperature is usually within the thermoneutral zone. We predict that abundance of terrestrial birds wintering in the Iberian Peninsula should show a positive relationship with minimum temperature. Accordingly, the average of the preferred temperatures that maximizes winter bird abundance should be higher than the average temperature registered during the study period in the region of analysis, a signal that the reduction of thermoregulation costs is important shaping winter bird distributions.

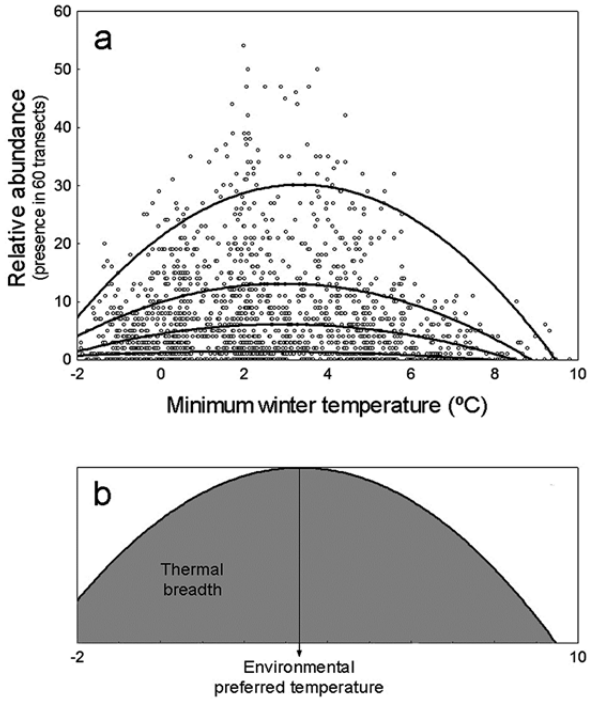

Figure 1. The preferred temperature and the thermal breadth of species are derived from quadratic quantile regression models on the abundance of species. (a) Abundance of *Columba palumbus* in relation to minimum winter temperature along 1689 UTM cells, and fitting equations for quantile regression models (from top to bottom: models on 0.95, 0.75, 0.5 and 0.25 percentiles). Abundance is the number of 15 min. transects over 60 in which the specie is detected at each UTM 10x10Km cell. (b) Representation of parameters of interest predicted by quantile regression model for percentile 0.95 of the example in (a). Environmental preferred temperature is the temperature at which the maximum abundance of the specie is predicted. Thermal breadth is the standardized area under the curve from -2 to 10ºC of quantile regression equations (shaded area in b).

A second goal is to test if the parameters describing the actual responses of species abundance to temperature are stable between climatic models (including temperature and precipitation) and models also including land cover, topographic and spatial predictors that are relevant to the biology of the studied species, considering their habitat preferences and biogeographic patterns. Our main interest is to quantify the biases assumed by bioclimatic models that do not control for the effects of other environmental variables, which may help to assess the consequences of not including these variables in forecasting the effects of climate change.

Methods

Bird abundance and environmental data

Field data were obtained from the national-scale project conducted by SEO/BirdLife to perform the first Spanish Atlas of Winter Birds (SEO/BirdLife, 2012). Relative abundance of each species at 1,689 UTM 10x10 km^2 cells was calculated as the frequency of occurrence in the sixty 15-min transects throughout the three winters (see a summary of the methods in the Spanish Atlas of Winter Birds in the Appendix S1 in Supporting Information). We selected 106 wintering bird species for the analyses, excluding nocturnal and aquatic birds, species that were detected in less than 40 UTM 10x10 km cells, and those that were rare or very difficult to detect (i.e., those with a maximum recorded frequency of occurrence lower than 0.05, or three 15-min transects per 60 transects censused).

The environmental characteristics of each UTM cell were described considering

the following variables: mean altitude and altitudinal range, average winter minimum temperature and winter precipitation, nine environmental gradients obtained using principal components analysis on 48 categories of land cover, and landscape diversity (for more details see the Appendix S1).

Data analyses

Quantile regressions were carried out using the higher 5% of the data (i.e., $\tau = 95^{th}$ percencile) to explore the upper limits of the relationships between bird abundance and temperature in the 106 studied species (for more details see Cade & Noon, 2003 and references therein). To account for non-linear effects of temperature, precipitation, land cover, landscape diversity, mean altitude and altitudinal range, we defined the linear and quadratic terms of these variables. To account for the influence of large-scale distribution patterns of species we also defined the three-order polynomial terms of latitude and longitude ($x+y+x*y+x^2+y^2+x^2*y+x*y^2+x^3+y^3$; Legendre, 1993). In order to obtain standardized regression coefficients (i.e., β's) and to avoid the undesirable relationship between the linear, quadratic and cubic terms in the estimation of partial regression coefficients, all the original variables were standardized to mean = 0 and sd = 1 prior to the calculus of squared and cubic predictors and data analyses (Schielzeth, 2010). Three different subsets of variables, and thus models, were used with each one of the 106 terrestrial bird species analyzed: climate models (CL hereafter) including the linear and quadratic terms of minimum temperature and precipitation; environmental models (ENV hereafter) including the linear and quadratic terms of the nine land cover components, landscape diversity, average altitude, altitudinal range, and the three-order polynomial terms of latitude and longitude; and finally the complete model (CL+ENV hereafter) including all variables. These three alternative quantile-regression models were compared within each species using the Akaike's index (AIC, Burnham & Anderson, 2002). A model was considered the best when ΔAIC = 0 and ΔAIC of other models were > 7. Two models were considered indistinguishably good when both ΔAIC < 2, and similarly good when both ΔAIC ≤ 7.

The regression model, $A = a + bT + cT^2$, was used to parameterize the partial influence of temperature (T) on bird abundance (A) after the simultaneous consideration of the remaining predictors included in CL and CL+ENV models. The temperature at which the maximum abundance of each specie is predicted (environmental preferred temperature, T_{PREF}) was calculated by solving the equation $dA \cdot dT^{-1} = 0$. The thermal span of the species (thermal breadth, $T_{BREADTH}$) was obtained by integrating $A \cdot dT$ between -2 and 10ºC, standardizing the maximal abundances of all species to 1.

The partial regression coefficients b and c, the environmental preferred temperature and the thermal breadth of species were compared between CL and CL+ENV models using Pearson correlations and paired t-tests (see Appendix S2 in Supporting Information). All data analyses were carried out with Gretl scripts (release 1.9.5, http://gretl.sourceforge.net/).

Results

In 100 out of 106 species studied (94.3%) CL+ENV models including all predictor variables provide the lowest AIC figures. In the remaining 6 species, the lowest AIC figures are obtained for models including only environmental variables (ENV models), although ΔAIC figures for CL+ENV models are lower than 4.1 (i.e., relatively similar plausibility). In 92 out of 106 species, AIC of CL+ENV models was smaller in more than 10 units than AIC for ENV models. In all species, ENV models are considerably better than models including only climatic variables (CL models), with ΔAIC of ENV vs. CL models higher than 80 (see Appendix S3 in Supporting Information for more details). The proportional increase

Table 1. **Bioclimatic models disregarding relevant environmental variables (CL models) overestimate the influence of temperature on species abundance (b coefficient) and underestimate the thermal plasticity of species (thermal breadth)**. Climatic models (CL) that include minimum winter temperature and cumulative winter precipitation are compared to CL+ENV models that also account for land cover, topography and spatial location. Figures are parameter averages obtained from 95%-quantile regression models on the partial effect of minimum winter temperature on the relative abundance of 106 bird species wintering in peninsular Spain, sampled at 1689 UTM 10x10 km^2 cells in three consecutive winters (2008-2011). **b**, **c**: linear and quadratic regression coefficients; $\mathbf{T_{PREF}}$: the winter minimum temperature that maximizes the relative abundance of the species; $\mathbf{T_{BREADTH}}$: area under the curve defined by the second order polynomial equation that relates the abundance of species to the temperature using the coefficients **b** and **c**. Detailed data for all species are shown in Appendix S2. Degrees of freedom for t tests are 105.

	CL models		CL+ENV models			
	mean	sd	mean	sd	t	p
Standardized linear coefficient, **b**	1.89	4.71	0.30	1.67	3.56	<0.001
Standardized curvilinear coefficient, **c**	-0.16	1.34	-0.09	0.68	0.62	0.533
Env. preferred temperature **(ºC)**, $\mathbf{T_{PREF}}$	4.78	5.06	5.26	4.69	0.77	0.445
Thermal breadth, $\mathbf{T_{BREADTH}}$	0.64	0.20	0.71	0.19	3.38	0.001

in explained deviance derived from the addition of temperature and precipitation to ENV models (from ENV to CL+ENV models in 95%-quatile regressions) ranged between 0.2 to 29%, with an average of 4.3% (sd = 4.3 %, n = 106 spp). Therefore, models with climate only variables have considerably lower explanatory power describing actual spatial variation in abundance of wintering birds than models including landscape and topographic variables. The addition of climatic variables to models with land cover, habitat diversity, topographic and spatial predictors increases the strength of evidence of the models analyzing the spatial variation of winter bird abundance, although the increase in the explained variability is of low magnitude.

Standardized lineal coefficients **b** describing the relationship between minimum winter temperature and bird abundance in 106 species are on average positive for both climatic only and CL+ENV models, but are significantly higher in CL models than in CL+ENV models (paired *t* test: t = 3.56, df = 105, p < 0.001; Table 1). The quadratic term **c** shows predominantly negative values, defining a hump-shaped relationship between temperature and the relative abundance of bird species; the standardized coefficients **c** are not significantly different comparing CL and CL+ENV models (paired *t* test: t = 0.62, df = 105, p = 0.533). Standardized linear regression coefficients **b** of temperature have larger absolute values than the quadratic terms **c** in both CL and CL+ENV models (Table 1; paired *t* test comparing the absolute figures of standardized coefficients **b** and **c**; CL models: t = 6.86, df = 105, p << 0.001; CL+ENV models: t = 5.99, df = 105, p << 0.001). Therefore, the linear increase of relative abundance with winter temperature is, on average, positive and more important than the curvilinear pattern, and its effect fades when other environmental variables are considered.

Standardized regression coefficients for temperature in CL models are loosely associated with coefficients obtained in CL+ENV models (Figure 2). The correlation between the linear term **b** in CL and CL+ENV models is positive and significant, but accounts for a very low proportion of shared variance (R^2 = 0.06, p = 0.011). A more intense association between CL and CL+ENV models is observed for the quadratic coefficient **c** defining a curvilinear relationship between temperature and the relative abundance of species (R^2 = 0.34. p << 0.001).

The environmental preferred temperature that maximizes the relative abundance of species ($\mathbf{T_{PREF}}$) is on average 4.8 ºC for 106 species in CL models, and 5.26 ºC in CL+ENV models (Table 1); the difference between both figures is not significantly different between CL and CL+ENV models (paired *t* test: t = 0.77, df = 105, p = 0.445), and both estimates are non-significantly correlated (R^2 = 0.017, p = 0.177; Figure 2). The average figure of $\mathbf{T_{PREF}}$ is significantly higher than the average temperature available in winter in peninsular Spain (2.55 ºC), in both CL (t-test: p << 0.001), and CL+ENV models (p << 0.001). $\mathbf{T_{PREF}}$ is lower than 0ºC in 30 out of 106 species in CL models, and in 19 species in CL+ENV models (i.e., preferences for colder areas; e.g., *Dryocopus martius*, *Cinclus cinclus*, *Turdus pilaris*, *Corvus corone*, *Fringilla montifringilla*, *Emberiza cia*), while it is higher than 5ºC in 53-54 species in both CL and CL+ENV models (i.e., preferences for warmer areas; e.g., *Elaneus caeruleus*, *Upupa epops*, *Alcedo atthis*, *Streptopelia decaocto*, *Ptynoprogne rupestris*, *Phylloscopus collybita*, *Cisticola juncidis*, *Lanius meridionalis*).

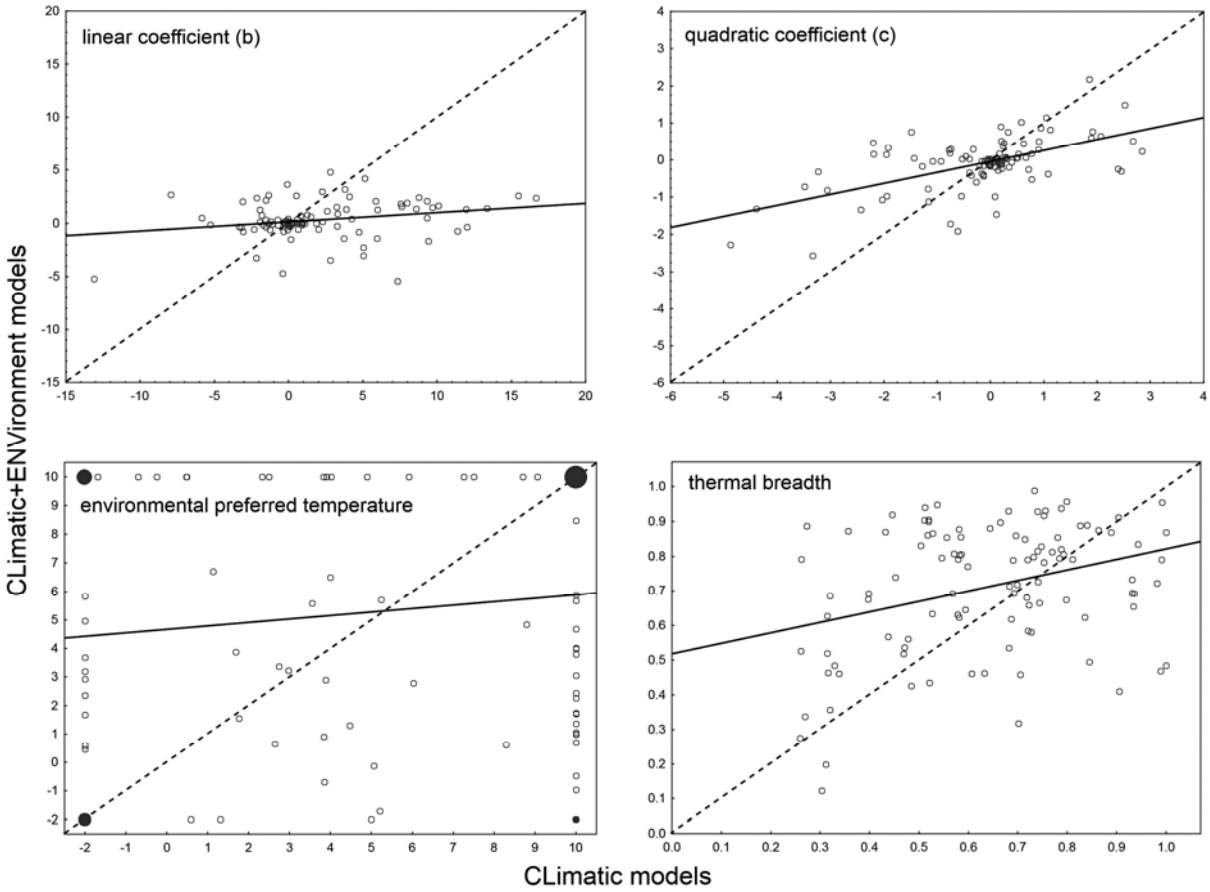

Figure 2. The effect of temperature on the winter abundance of 106 bird species change from CL models to CL+ENV models. Climatic models (CL) include minimum winter temperature and cumulative winter precipitation, while CL+ENV models also account for land cover, topography and spatial location. Standardized linear coefficient (**b**) and standardized quadratic coefficient (**c**) refer to the relationship between relative abundance and winter minimum temperature using 95%-quantile regressions; environmental preferred temperature is the winter minimum temperature at which the relative abundance of the species is highest; thermal breadth is the area under the curve defined by the equation that relates the abundance of species to the temperature using the coefficients **b** and **c**. Solid line represents the linear fitted equation of the interspecific variation of parameters derived from CL and CL+ENV models; dashed line represents the identity of the results derived from the two models. Solid circles denote several overlapped species (3, 8, 10 and 19 spp). Detailed data for all species are shown in Appendix S2.

The thermal breadth ($T_{BREADTH}$), defined as the relative area under the curve of the functional response of abundance with temperature, is significantly lower in climatic (CL) than in CL+ENV models (paired *t* test: t = 3.38, df = 105, p = 0.001), and both estimates are scarcely correlated ($R^2 = 0.106$, $p < 0.001$). Therefore, bird species appear to be more stenotopic in their response to temperature when only climatic variables are considered than when considering also land cover, topographic and spatial variables.

Discussion

Wintering birds are more abundant at warmer environments

Globally, birds wintering in the Iberian Peninsula do not distribute randomly throughout the available thermal space. There is a preponderance of positive relationships between temperature and species abundance (see positive average linear coefficients; Table 1), and on average species select to live in areas 2.9 ºC warmer than temperature available in winter in peninsular Spain. This is in accordance with a winter restrictive scenario with temperatures well below the thermoneutral zone, where metabolic costs of birds increase linearly at decreasing temperatures (Calder & King, 1974; Kendeigh et al., 1977).

Most species show triangular-shaped (see example in Figure 1 and data in Appendix S2). However, the importance of temperature in determining winter bird distribution depends on the species, as there is a broad range of versatility of how species utilize the available winter thermal space (i.e., the thermal breadth of the studied species varies from 0.225 to 0.975; Appendix S2; Moussus et al., 2011). Our results suggest that winters will be less restrictive for birds wintering in the Iberian peninsula under future climate warming scenarios (IPCC, 2007; Brunet et al., 2009), though the impact of changes will depend on species-specific thermal plasticity, and will be more intense in those species with a narrow thermal breadth that prefer higher winter temperatures and that mainly rely on arthropods and fruits as winter food (e.g., *Alcedo atthis, Upupa epops, Ptynoprogne rupestris, Luscinia svecica, Cisticola juncidis, Phylloscopus collybita, Sylvia melanocephala, Carduelis chloris, Serinus serinus*). Future studies should explore the biological traits associated with interspecific differences in winter thermal preferences, considering the phylogenetic relatedness and differences among species in body mass, habitat selection, diet, metabolic characteristics and biogeographic origins.

More than climate: assessing the biases of bioclimatic models

Here we contribute to the open debate about the usefulness of bioclimatic models by providing quantitative evidence of their limitations (Hampe, 2004; Pearson & Dawson, 2004; Jeschke & Strayer, 2008; Araujo & Peterson, 2012). The position and breadth of species in the thermal gradient is highly dependent upon whether they are estimated using only climatic variables, or the partial influence of temperature after controlling for other environmental variables accounting for habitat preferences, position within altitudinal gradients and broad-scale patterns related to pure spatial effects. Moreover, the estimations obtained from CL and CL+ENV models only share c. 11% of observed interspecific variability. To our knowledge, this is the first study quantifying the consequences of not controlling for a large variety of environmental factors when addressing the parameterization of the relationship between temperature and spatial variation in species abundance (but see similar approaches on future predictions based on presence-absence data in Luoto & Heikkinnen, 2008; Sormunen et al., 2011 and Barbet-Massin et al., 2012). We also find that controlling for other environmental variables not only improves models on the spatial variation of bird abundance, but also drastically modifies the postulated effects of temperature on species distributions.

We demonstrate that a major risk of oversimplifying models is to infer highly biased descriptions of the thermal preferences of species, suggesting birds to be more responsive to temperature than they actually are (Table 1). Specifically, if we do not control for topographic and habitat preferences of species within their geographical extents, we are overestimating both the influence of temperature on species abundance and the thermal specialization of species (i.e., higher **b** and **c** coefficients and lower thermal breadths predicted in climatic-only models). Therefore, bioclimatic models only considering climatic variables might inflate the importance and the magnitude of global warming effects, when in fact temperature is not so deterministic and birds are probably more able to deal with changes than have been previously assumed. Contrary to Pearson & Dawson (2003), we consider that conclusions drawn from models including only climate would give information of doubtful utility, at least at medium latitudes and at lower resolutions of 100 km^2 working with animal abundance (Thuiller et al., 2004; Luoto et al., 2007; Jetz et al., 2007).

Moreover, using a very simplistic model based on temperature and precipitation will result in highly imprecise predictions about the thermal preferences of species. The environmental preferred temperatures estimated by CL models are considerably different than those estimated by CL+ENV models (an average within species difference of 4.3 ºC, and more than 2 ºC for 63% of the studied species; see Appendix S2 and Figure 2). This estimation bias obtained when not controlling for other relevant environmental factors is similar to the magnitude of the temperature increase forecasted from 2010 to 2070 (1.0–2.5 ºC under A2 and B2 scenarios; Brunet et al., 2009). In a similar vein, Bakken and Anguilletta (2013) have shown the importance of good procedures for estimating and modeling thermal environments, because errors in measured operative temperature similar in amount to changes in temperature predicted under climate warming would reduce the value of research efforts.

Likewise, the estimated thermal breadth differ an average of 20% between CL and CL+ENV models. These discrepancies may result from the surrogate character of temperature, because the shape of the response of species abundance or occurrence to temperature in climatic-only models probably contains the response to other environmental factors directly related to species-specific habitat or trophic preferences (e.g., low temperatures in alpine habitats, warmer temperatures in Mediterranean 'dehesas' than in coniferous forests, high temperatures in diversified agricultural areas with olive groves, vineyards or irrigated lands; high arthropod and fruit availability in warmer areas). It is highly likely that climate-only models (e.g., Huntley et al., 2007; Araujo et al., 2012) will produce a distorted picture of the influence of temperature in determining actual bird distributions, and thus future changes in distribution and abundance. We think this issue should be resolved before forecasting species distributions under either current or future scenarios of global warming (Hampe, 2004; Heikkinen et al., 2006; Luoto & Heikkinnen, 2008; Sormunen et al., 2011 and Barbet-Massin et al., 2012).

In all species, models only including climatic variables are much worse than any other model including the effect of land cover, topography and spatial position (according to both AICc figures and the proportion of explained deviance, Appendix S3; see also Rahbeck & Graves, 2001; Pearson et al., 2004; Seoane et al., 2004; Luoto & Heikkinen, 2008; Sormunen et al., 2011; Triviño et al., 2011; Barbet-Massin et al., 2012; Tingley et al., 2012). Moreover, adding temperature and precipitation to other environmental variables does not improve models for one third of the studied species. This is surprising considering that we use the minimum temperature that is mainly registered during the long winter nights, and that winter habitat preferences are relaxed because birds adopt a vagabonding lifestyle

exploring a greater variety of habitats over larger areas to track the spatial and temporal distribution of food availability (Levey & Stiles, 1992; Wiktander et al., 2001). The effect of temperature might be even less pronounced when considering other scenarios such as the breeding season, when average environmental temperatures lay within the thermoneutral zone (18-22 to 33-40 ºC for a broad variety of species, Calder & King, 1974; Kendeigh et al., 1977), and possible overheating can be avoided by sheltering in the shade.

Variables that have been proved to be of functional relevance for a certain group of organisms under current conditions must be considered when predicting their future distributions (Kissling et al., 2010; Sormunen et al., 2011). But sadly, relevant variables related to habitat preferences of species are frequently overlooked because it is very difficult to predict their trends (e.g., changes in future land cover; Settele et al., 2005; Busch, 2006; Rounsevell et al., 2006; Spangenberg et al., 2012) due to an unavoidable high uncertainty inherent to future human-related processes (Verburg et al., 2011). At best, the fate of biodiversity has been forecasted using these uncertain future land cover scenarios (Pompe et al., 2008; Barbet-Massin et al., 2012; Schweiger et al., 2012), or predicted changes in potential vegetation cover of particular tree species not very relevant for habitat preferences of species (Triviño et al., 2011). Even in these cases, predictions of future biodiversity distributions should be taken carefully (Martin et al. 2013). Ignoring relevant environmental variables or including very coarse landscape-habitat categories may result in biased models that overestimate the effect of temperature on species abundances, and could underestimate the plasticity of species in responding to global warming.

Conclusions

We found that climatic models not accounting for habitat, topographic and spatial preferences of species may incur in strong biases when parameterizing the response of birds to temperature. The main consequence of disregarding these variables is that the influence of temperature on species abundance is overestimated and the breadth of species within thermal gradients is underestimated. Under either current or future warming scenarios, we should only take up the appealing challenge of predicting species distribution when able to consider relevant biological traits affecting the distribution of organisms (e.g., habitat and food preferences) or environmental surrogates related to those traits, and not only "big data".

Aknowledgements

This paper is a contribution to projects CGL2008-02211/BOS and CGL2011-28177/BOS of the Spanish Ministry of Education and Science. Juan Carlos del Moral (SEO / BirdLife) provided the raw data from the Winter Spanish Bird Atlas. David Palomino was contracted by SEO / BirdLife to organize, design, analyze and develop the Winter Spanish Bird Atlas. We also thank Jorge M. Lobo for helpful comments on a first draft of the paper and C. Jasinski for improving the English of the manuscript.

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Supporting Information

Appendix S1. Description of the Spanish Bird Atlas of Winter Birds.

Appendix S2. Parameters from abundance models.

Appendix S3. Best model selection by AIC criterion

Appendix S1

Bird abundance and environmental data

Hundreds of experienced birdwatchers were asked to sample UTM cells following a standardized methodology during three consecutive winters (2007-2010, from mid-November to mid-February), in order to map the distribution and relative abundance of each species throughout peninsular Spain. The sample unit was the 10x10 km UTM cell, so that participants had to accumulate a minimum survey of 15 h per cell, divided in 60 line transects of 15-min, and covering all the habitats present in proportion to their extent in the 100 km^2 (previously calculated by means of GIS tools). All the individual birds detected were separately noted for each 15-min transect. The final sample size was 1,689 UTM cells, c. 80% out of 2,121 UTM cells covered in the Atlas, after discarding those with too little sampling effort (less than 60 line transects per 100 Km^2 in the three winters), and low land surface in peninsular Spain (<50 Km^2).

The environmental characteristics of each UTM cell were obtained from updated GIS data covering the whole Iberian Peninsula, provided by the cartographic divisions of different environmental Spanish agencies (www.marm.es; www.aemet.es). The spatial location was defined by latitude and longitude coordinates of the UTM cell centers. Topographic variables (mean altitude and altitudinal range) were obtained from a digital elevation model at a 200 m resolution. Climatic variables were calculated as the daily averages (minimum temperature) or summatory (precipitation) during the period of study (mid-November to mid-February 2007-2010). Land cover variables were estimated from the percentage cover of main land-uses, ranging from dense forests to almost bare habitats, and from pristine landscapes to heavily urbanized cities (Inventario Nacional Forestal III, 2007-2008, Spanish Ministerio de Medio Ambiente). Forty-eight categories of land cover were considered with a special emphasis on distinguishing different woodlands and agricultural habitats of major quantitative importance throughout Spain. These forty-eight categories were subsequently reduced to 14 major categories according to their similarities: coniferous forests (of several *Pinus* species and *Abies alba*), deciduous forests (*Fagus sylvatica* and several oaks species, mainly *Qercus robur*, *Q. petraea*, *Q. pyrenaica*, *Q. pubescens* and *Q. faginea*), mixed forests (with coniferous and deciduous trees), sclerophyllous forests (dominated by *Q. rotundifolia*, *Q. ilex* and *Q. suber*), open forests of several *Juniper* species (*J. thurifera* and *J. oxycedrus*), parklands or '*dehesas*' (open woodlands dominated by *Q. rotundifolia*, *Fraxinus* spp. or other deciduous trees), riverside and lagoon vegetation, shrublands, grasslands and pasturelands, dry herbaceous croplands (mainly ploughed fields and fallow lands in the winter season), irrigated herbaceous croplands, wooded agricultural areas (dominated by fruit or olive trees), agricultural mosaics (including vineyards, irrigated fields, etc.), and urban-industrial areas. These land cover categories were defined according to habitat preferences of birds during the winter season considering the recent literature on wintering birds in the Iberian Peninsula (Herrando et al., 2011; SEO/BirdLife, 2012). A principal components analysis (PCA) with a varimax rotation was carried out with these 14 land cover categories describing the 1689 UTM cells to obtain a reduced number of factors that summarized the relationships among variables, and to define environmental gradients within the study region. Nine factors with eigenvalues higher than one were obtained, which accounted for 87.7% of original variance in the 14x1689 landscape matrix. For more details see Carrascal & Palomino (2012). Finally, the Shannon index with the 14 landscape categories was estimated to account for the landscape diversity of each UTM cell.

Appendix S2.

Parameters from abundance models obtained for 106 terrestrial bird species wintering in the Iberian Peninsula, corresponding to winter censuses on 1689 10x10 km^2 UTM (years 2008-2011). Climatic models (CL): quadratic polynomial relationship between the relative abundance of each species and winter minimum temperature in a 95%-quantile regression model also including the linear and quadratic terms of precipitation as predictor variables. CL+ENV models: quadratic polynomial relationship between the relative abundance of each species and winter minimum temperature after controlling for other environmental variables (three-order polynomial of geographical position, and linear and quadratic terms for average altitude, altitudinal range, nine land cover components and landscape diversity). a, b, c: intercept, standardized linear term and standardized quadratic regression coefficients. T_{PREF}: environmental preferred temperature (i.e., minimum winter temperature at which the maximum abundance of the specie is predicted); T_{BREADH}: thermal breadth (i.e., area under the curve from -2 to 10ºC of 95%-quantile regression equations with the maximum abundance of each species relativized to 1). #UTM: number of 10x10 km^2 UTM cells where the species were present.

		CL models				CL+ENV models			
Spp	**# UTM**	**b**	**c**	**T_{PREF} (ºC)**	**$T_{BREADTH}$**	**b**	**c**	**T_{PREF} (ºC)**	**$T_{BREADTH}$**
Accipiter gentilis	261	-0.076	-0.048	0.6	0.83	-0.074	0.015	-2.0	0.89
Accipiter nisus	804	0.000	0.000	1.7	1.00	0.150	-0.141	3.9	0.87
Aegithalos caudatus	1352	0.134	-1.944	2.6	0.78	-1.495	-0.973	0.7	0.79
Aegypius monachus	185	0.578	-0.529	3.9	0.68	0.392	0.029	10.0	0.71
Alauda arvensis	1121	2.269	-0.131	10.0	0.86	2.985	-0.405	10.0	0.88
Alcedo atthis	218	0.900	0.113	10.0	0.43	0.052	0.013	10.0	0.87
Alectoris rufa	1298	9.414	-2.033	8.3	0.72	-1.684	-1.074	0.6	0.79
Anthus pratensis	1426	10.082	-1.921	9.1	0.74	1.655	0.324	10.0	0.81
Anthus spinoletta	199	-0.008	-0.001	-2.0	0.98	-0.096	-0.057	0.5	0.72
Aquila chrysaetos	384	0.001	-0.008	2.7	0.99	0.112	-0.171	3.4	0.79
Burhinus oedicnemus	177	0.912	0.136	10.0	0.40	0.127	0.032	10.0	0.68
Buteo buteo	1372	-1.715	-0.762	-0.2	0.74	-0.144	0.178	10.0	0.93
Carduelis cannabina	1373	5.952	2.450	10.0	0.58	-1.433	-0.300	-2.0	0.79
Carduelis carduelis	1591	7.979	2.516	10.0	0.59	1.903	1.479	10.0	0.65
Carduelis chloris	1362	5.044	1.854	10.0	0.48	-2.250	2.178	10.0	0.43
Carduelis spinus	728	0.519	0.325	10.0	0.70	2.601	0.748	10.0	0.46
Certhia brachydactyla	1094	-1.543	1.078	-2.0	0.80	0.348	-0.384	3.7	0.96

Certhia familiaris	44	-0.004	0.002	-2.0	0.85	0.004	-0.014	2.9	0.49
Cettia cetti	704	2.027	0.207	10.0	0.55	-0.552	-0.226	-0.5	0.80
Cinclus cinclus	176	-0.719	0.308	-2.0	0.33	-0.188	0.027	-2.0	0.48
Circus aeruginosus	286	0.905	0.193	10.0	0.52	-0.153	-0.128	1.1	0.90
Circus cyaneus	568	-0.028	0.169	10.0	0.75	0.121	0.166	10.0	0.78
Cisticola juncidis	482	4.250	2.069	10.0	0.32	0.425	0.648	10.0	0.46
Coccothraustes coccothraustes	359	-0.727	0.206	-2.0	0.63	0.336	0.506	10.0	0.46
Columba livia	908	3.263	-0.359	10.0	0.67	-0.280	-0.409	1.7	0.90
Columba oenas	205	-0.034	0.010	-2.0	0.93	-0.223	-0.140	0.6	0.69
Columba palumbus	1377	5.128	-4.386	4.0	0.71	4.195	-1.315	6.5	0.85
Corvus corone	1090	-13.107	1.886	-2.0	0.34	-5.187	0.599	-2.0	0.46
Corvus corax	1151	-1.192	0.192	-2.0	0.80	0.156	0.896	10.0	0.67
Corvus monedula	466	1.094	-0.130	10.0	0.75	-0.016	-0.164	2.4	0.92
Cyanopica cooki	410	2.274	-2.200	3.8	0.77	0.153	0.466	10.0	0.81
Dendrocopos major	1026	-3.330	0.523	-2.0	0.51	-0.293	0.162	-2.0	0.94
Dendrocopos minor	109	0.136	-0.169	3.6	0.68	0.080	-0.033	5.6	0.93
Dryocopus martius	56	-0.246	0.136	-2.0	0.31	-0.054	0.028	-2.0	0.20
Elanus caeruleus	126	0.523	-0.050	10.0	0.60	0.079	0.018	10.0	0.77
Emberiza calandra	1096	7.611	-0.929	10.0	0.70	1.550	-0.033	10.0	0.86
Emberiza cia	1105	-2.168	0.896	-2.0	0.72	-3.223	0.275	-2.0	0.58
Emberiza cirlus	934	-1.345	-1.173	1.1	0.72	2.618	-0.781	6.7	0.68
Emberiza citrinella	317	-1.939	0.492	-2.0	0.27	0.105	0.053	10.0	0.34
Emberiza schoeniclus	305	0.406	0.176	10.0	0.52	0.044	-0.109	3.1	0.86
Erithacus rubecula	1604	8.781	-3.229	5.9	0.84	2.412	-0.319	10.0	0.89
Falco columbarius	303	-0.147	-0.043	-1.7	0.81	0.251	-0.036	10.0	0.79
Falco peregrinus	283	0.000	0.000	3.9	1.00	0.045	-0.164	2.9	0.48
Falco tinnunculus	1310	1.238	0.939	10.0	0.58	0.785	0.859	10.0	0.63
Fringilla coelebs	1649	2.824	-1.436	5.0	0.94	-3.435	0.047	-2.0	0.84
Fringilla montifringilla	332	-1.104	0.280	-2.0	0.36	-0.102	0.051	-2.0	0.87
Galerida cristata	1131	11.364	-1.164	10.0	0.64	-0.739	-1.121	1.7	0.88

Galerida theklae	720	7.346	-0.620	10.0	0.61	-5.414	-1.907	-1.0	0.46
Garrulus glandarius	1098	-2.134	-1.282	0.5	0.74	2.366	-0.165	10.0	0.73
Grus grus	193	1.493	-0.393	7.3	0.73	0.622	0.024	10.0	0.80
Gyps fulvus	800	-1.942	-0.740	-0.7	0.70	1.249	0.295	10.0	0.72
Hieraaetus fasciatus	96	0.341	-0.037	10.0	0.59	0.028	-0.028	3.8	0.81
Lanius meridionalis	1048	3.876	-0.781	8.7	0.74	1.307	0.270	10.0	0.67
Loxia curvirostra	393	-1.539	2.395	10.0	0.45	-0.357	-0.238	0.7	0.92
Lullula arborea	881	4.739	-3.064	4.5	0.75	-0.829	-0.818	1.3	0.83
Luscinia svecica	44	0.345	0.284	10.0	0.26	0.084	0.071	10.0	0.27
Melanocorypha calandra	535	1.869	0.142	10.0	0.73	-0.020	-0.086	2.3	0.99
Milvus milvus	794	-1.815	-1.083	0.5	0.76	0.763	-0.037	10.0	0.93
Monticola solitarius	223	0.963	0.140	10.0	0.40	0.097	-0.082	4.0	0.69
Motacilla alba	1495	12.012	0.141	10.0	0.54	-0.348	-0.278	1.0	0.95
Motacilla cinerea	690	0.631	-0.097	10.0	0.84	-0.553	-0.028	-2.0	0.62
Oenanthe leucura	145	0.849	0.393	10.0	0.31	-0.076	-0.060	1.0	0.52
Otis tarda	143	-0.001	-0.005	2.3	0.99	-0.015	0.028	10.0	0.95
Parus ater	934	-7.938	2.840	-2.0	0.45	2.660	0.232	10.0	0.74
Parus caeruleus	1426	2.605	-2.195	4.0	0.89	1.159	0.157	10.0	0.87
Parus cristatus	905	-5.843	2.669	-2.0	0.50	0.493	0.516	10.0	0.83
Parus major	1614	3.788	-0.753	8.8	0.90	3.168	-1.715	4.8	0.91
Parus palustris	141	-0.327	0.131	-2.0	0.56	0.114	-0.059	5.0	0.85
Passer domesticus	1553	9.333	-0.133	10.0	0.58	2.076	-0.435	8.5	0.88
Passer hispaniolensis	231	3.224	-0.330	10.0	0.58	1.526	0.292	10.0	0.62
Passer montanus	667	-0.040	0.713	10.0	0.53	0.434	-0.252	4.7	0.87
Petronia petronia	586	-3.054	1.917	-2.0	0.44	-0.759	0.770	10.0	0.57
Phoenicurus ochruros	1389	9.701	-0.264	10.0	0.52	1.492	-0.592	5.7	0.91
Phylloscopus collybita	1316	11.948	1.048	10.0	0.53	1.324	1.139	10.0	0.63
Pica pica	1353	5.047	-4.874	3.8	0.72	-3.029	-2.271	0.9	0.66
Picus viridis	1201	-0.395	-0.393	1.3	0.91	-4.680	-0.347	-2.0	0.41
Prunella collaris	70	-0.236	0.171	-2.0	0.31	0.141	-0.053	5.8	0.63

Prunella modularis	865	0.822	-2.434	3.0	0.69	0.725	-1.342	3.2	0.69
Pterocles alchata	86	0.029	-0.028	3.9	0.93	-0.282	-0.107	-0.7	0.65
Pterocles orientalis	150	0.081	-0.040	5.1	0.94	-0.288	-0.133	-0.1	0.69
Ptyonoprogne rupestris	366	3.292	1.121	10.0	0.32	0.867	0.815	10.0	0.36
Pyrrhocorax pyrrhocorax	463	-0.354	-0.550	1.8	0.70	-0.780	-0.968	1.6	0.32
Pyrrhocorax graculus	60	-0.001	0.000	-2.0	0.99	-0.021	-0.030	1.7	0.47
Pyrrhula pyrrhula	402	-1.258	0.504	-2.0	0.52	-0.605	0.062	-2.0	0.43
Regulus ignicapilla	1123	-0.089	-1.955	2.5	0.73	3.636	0.150	10.0	0.58
Regulus regulus	492	-3.194	0.912	-2.0	0.32	-0.384	0.504	10.0	0.69
Remiz pendulinus	63	0.224	0.126	10.0	0.27	0.034	-0.029	4.0	0.89
Saxicola rubicola	1365	8.586	-0.466	10.0	0.58	1.336	0.094	10.0	0.80
Serinus citrinella	114	-1.352	0.657	-2.0	0.26	-0.002	0.058	10.0	0.79
Serinus serinus	1224	15.483	0.350	10.0	0.57	2.604	-0.195	10.0	0.81
Sitta europaea	640	-0.051	0.618	10.0	0.79	-0.623	0.439	-2.0	0.82
Streptopelia decaocto	911	5.854	0.240	10.0	0.47	2.090	0.373	10.0	0.52
Sturnus unicolor	1445	7.558	-3.485	5.2	0.79	1.838	-0.721	5.7	0.94
Sturnus vulgaris	629	4.102	0.081	10.0	0.48	2.515	-0.191	10.0	0.56
Sylvia atricapilla	1000	13.376	0.773	10.0	0.51	1.414	-0.525	5.9	0.90
Sylvia melanocephala	922	16.664	0.579	7.5	0.57	2.395	1.026	10.0	0.69
Sylvia undata	1096	3.740	0.106	10.0	0.69	-1.401	-1.459	1.4	0.62
Tetrax tetrax	120	0.229	-0.107	5.2	0.78	-0.090	-0.026	-1.7	0.85
Troglodytes troglodytes	1052	-3.086	-0.206	-2.0	0.69	2.030	-0.155	10.0	0.79
Turdus iliacus	712	-1.522	-0.166	-2.0	0.68	2.178	-0.360	10.0	0.53
Turdus merula	1634	2.808	-1.483	4.9	0.93	4.785	0.748	10.0	0.73
Turdus philomelos	1488	9.337	-3.330	6.0	0.79	0.500	-2.565	2.8	0.81
Turdus pilaris	372	-2.322	0.773	-2.0	0.26	-0.540	0.170	-2.0	0.53
Turdus torquatus	58	-0.296	0.208	-2.0	0.30	0.057	-0.109	3.2	0.12
Turdus viscivorus	1206	-5.258	0.079	-2.0	0.59	-0.152	-0.989	2.4	0.86
Upupa epops	602	5.991	0.252	10.0	0.47	1.288	0.454	10.0	0.54

Appendix S3.

Best model selection by AIC criterion (Burnham and Anderson 2002) for abundance models of 106 species of terrestrial birds wintering in peninsular Spain, censused on 1689 10x10 Km UTM cells along three consecutive winters (2008-2011). Abundance was measured as the number of 15 min. transects in which the specie was detected over a total of 60 per UTM cell. CL models: only including winter minimum temperature and cumulative winter precipitation as predictor variables (with linear and quadratic terms); ENV models: including geographical position (three-order polynomial of latitude and longitude of each UTM cell), average altitude, altitudinal range, 9 principal components of land cover and landscape diversity (using linear and quadratic terms); CL+ENV models: including all predictors of CL and ENV models. A model is considered the best when ΔAIC = 0 and ΔAIC of other models > 7. Two models are considered indistinguishable good (=) when both ΔAIC < 2, and similarly good (≈) when both ΔAIC ≤ 7. % incr. deviance due to CL vars: proportional increase in the explained deviance accounted for ENV models due to the addition of the linear and quadratic terms of winter temperature and precipitation (expressed in percentage of increase with respect to the deviance explained by ENV models).

Spp	ΔAIC CL model	ΔAIC ENV model	ΔAIC CL+ENV model	BEST MODEL	% incr. deviance due to CL vars
Accipiter gentilis	434.6	0.0	3.2	CL+ENV ≈ ENV	0.8
Accipiter nisus	216.7	28.2	0.0	CL+ENV	14.8
Aegithalos caudatus	1398.0	86.5	0.0	CL+ENV	6.3
Aegypius monachus	1436.8	42.6	0.0	CL+ENV	2.7
Alauda arvensis	2404.6	35.8	0.0	CL+ENV	1.6
Alcedo atthis	1575.2	31.0	0.0	CL+ENV	1.9
Alectoris rufa	1193.0	26.8	0.0	CL+ENV	1.9
Anthus pratensis	1057.6	0.0	4.1	CL+ENV ≈ ENV	0.2
Anthus spinoletta	574.1	16.6	0.0	CL+ENV	3.8
Aquila chrysaetos	587.7	73.4	0.0	CL+ENV	12.1
Burhinus oedicnemus	524.7	13.3	0.0	CL+ENV	1.6
Buteo buteo	1042.7	91.4	0.0	CL+ENV	7.9
Carduelis cannabina	1024.9	6.4	0.0	CL+ENV	1.0
Carduelis carduelis	710.7	36.8	0.0	CL+ENV	3.4
Carduelis chloris	912.7	112.9	0.0	CL+ENV	7.9
Carduelis spinus	951.9	205.6	0.0	CL+ENV	22.0
Certhia brachydactyla	1460.8	23.9	0.0	CL+ENV	1.9
Certhia familiaris	1706.8	0.0	1.7	CL+ENV = ENV	0.3

Cettia cetti	1370.2	54.6	0.0	CL+ENV	4.2
Cinclus cinclus	865.7	29.3	0.0	CL+ENV	2.0
Circus aeruginosus	1391.3	0.0	1.7	CL+ENV = ENV	0.3
Circus cyaneus	1294.6	9.2	0.0	CL+ENV	1.0
Cisticola juncidis	1085.3	73.6	0.0	CL+ENV	3.2
Coccothraustes coccothraustes	752.7	44.4	0.0	CL+ENV	5.8
Columba livia	1462.3	20.5	0.0	CL+ENV	1.5
Columba oenas	349.6	23.9	0.0	CL+ENV	3.8
Columba palumbus	1389.9	125.6	0.0	CL+ENV	7.4
Corvus corone	1070.5	105.6	0.0	CL+ENV	6.2
Corvus corax	661.6	26.1	0.0	CL+ENV	4.4
Corvus monedula	640.2	14.8	0.0	CL+ENV	2.5
Cyanopica cyanus	1726.6	36.9	0.0	CL+ENV	1.8
Dendrocopos major	1098.6	65.2	0.0	CL+ENV	4.7
Dendrocopos minor	916.3	32.4	0.0	CL+ENV	3.5
Dryocopus martius	1811.7	35.7	0.0	CL+ENV	2.0
Elanus caeruleus	996.3	15.5	0.0	CL+ENV	1.8
Emberiza calandra	1457.7	36.6	0.0	CL+ENV	2.3
Emberiza cia	1266.1	63.8	0.0	CL+ENV	5.3
Emberiza cirlus	1066.0	95.7	0.0	CL+ENV	9.3
Emberiza citrinella	596.0	57.5	0.0	CL+ENV	6.5
Emberiza schoeniclus	915.7	10.0	0.0	CL+ENV	1.3
Erithacus rubecula	937.7	152.1	0.0	CL+ENV	9.1
Falco columbarius	565.7	15.9	0.0	CL+ENV	2.6
Falco peregrinus	111.8	31.5	0.0	CL+ENV	29.0
Falco tinnunculus	1293.6	26.8	0.0	CL+ENV	2.2
Fringilla coelebs	785.7	62.8	0.0	CL+ENV	7.7
Fringilla montifringilla	270.6	25.0	0.0	CL+ENV	5.3
Galerida cristata	1447.7	63.6	0.0	CL+ENV	3.3
Galerida theklae	902.9	106.7	0.0	CL+ENV	7.3

Garrulus glandarius	1490.6	147.1	0.0	CL+ENV	7.6
Grus grus	999.3	14.8	0.0	CL+ENV	1.8
Gyps fulvus	813.4	38.8	0.0	CL+ENV	4.9
Hieraaetus fasciatus	626.0	7.9	0.0	CL+ENV	1.3
Lanius meridionalis	1058.3	30.6	0.0	CL+ENV	2.2
Loxia curvirostra	2166.5	14.3	0.0	CL+ENV	0.9
Lullula arborea	1673.8	36.9	0.0	CL+ENV	2.3
Luscinia svecica	435.2	49.8	0.0	CL+ENV	5.6
Melanocorypha calandra	2219.4	5.9	0.0	CL+ENV	0.5
Milvus milvus	1516.4	2.3	0.0	CL+ENV	0.6
Monticola solitarius	643.2	23.1	0.0	CL+ENV	2.2
Motacilla alba	933.8	1.3	0.0	CL+ENV	0.4
Motacilla cinerea	743.6	58.2	0.0	CL+ENV	7.2
Oenanthe leucura	1586.3	55.2	0.0	CL+ENV	2.6
Otis tarda	1174.1	13.2	0.0	CL+ENV	1.2
Parus ater	2890.0	66.4	0.0	CL+ENV	2.0
Parus caeruleus	1875.0	12.2	0.0	CL+ENV	0.8
Parus cristatus	2542.4	10.0	0.0	CL+ENV	0.6
Parus major	1021.3	64.1	0.0	CL+ENV	5.6
Parus palustris	1595.0	136.9	0.0	CL+ENV	5.4
Passer domesticus	1211.4	15.7	0.0	CL+ENV	1.2
Passer hispaniolensis	1462.4	131.6	0.0	CL+ENV	7.6
Passer montanus	625.6	8.7	0.0	CL+ENV	1.4
Petronia petronia	536.4	26.6	0.0	CL+ENV	3.6
Phoenicurus ochruros	934.6	30.0	0.0	CL+ENV	1.4
Phylloscopus collybita	807.8	28.0	0.0	CL+ENV	1.4
Pica pica	1018.1	46.7	0.0	CL+ENV	3.3
Picus viridis	578.9	67.8	0.0	CL+ENV	12.4
Prunella collaris	952.7	35.8	0.0	CL+ENV	4.1
Prunella modularis	1234.3	175.8	0.0	CL+ENV	11.5

Pterocles alchata	756.9	11.5	0.0	CL+ENV	1.7
Pterocles orientalis	630.7	37.9	0.0	CL+ENV	3.7
Ptyonoprogne rupestris	811.4	126.5	0.0	CL+ENV	5.6
Pyrrhocorax pyrrhocorax	901.9	113.4	0.0	CL+ENV	12.7
Pyrrhocorax graculus	1353.9	70.0	0.0	CL+ENV	4.0
Pyrrhula pyrrhula	1170.1	26.6	0.0	CL+ENV	1.6
Regulus ignicapilla	1197.6	52.1	0.0	CL+ENV	3.2
Regulus regulus	1185.3	45.0	0.0	CL+ENV	2.8
Remiz pendulinus	601.2	0.0	1.7	CL+ENV = ENV	0.7
Saxicola rubicola	1003.4	74.2	0.0	CL+ENV	3.4
Serinus citrinella	1314.4	0.0	0.9	CL+ENV	0.4
Serinus serinus	847.7	34.9	0.0	CL+ENV	1.5
Sitta europaea	1687.3	42.1	0.0	CL+ENV	2.1
Streptopelia decaocto	910.9	41.7	0.0	CL+ENV	2.4
Sturnus unicolor	1154.0	49.1	0.0	CL+ENV	3.4
Sturnus vulgaris	1495.9	108.8	0.0	CL+ENV	5.7
Sylvia atricapilla	1516.5	30.0	0.0	CL+ENV	1.4
Sylvia melanocephala	1170.4	112.1	0.0	CL+ENV	4.2
Sylvia undata	1600.4	147.5	0.0	CL+ENV	9.0
Tetrax tetrax	908.6	4.5	0.0	CL+ENV	1.0
Troglodytes troglodytes	1396.0	191.4	0.0	CL+ENV	6.1
Turdus iliacus	819.2	61.5	0.0	CL+ENV	6.8
Turdus merula	679.6	92.0	0.0	CL+ENV	10.7
Turdus philomelos	788.7	97.1	0.0	CL+ENV	9.0
Turdus pilaris	603.9	15.2	0.0	CL+ENV	1.7
Turdus torquatus	1486.1	57.2	0.0	CL+ENV	4.2
Turdus viscivorus	1291.9	17.4	0.0	CL+ENV	1.5
Upupa epops	1458.2	45.8	0.0	CL+ENV	1.9

Integrative remarks

Integración de resultados

Integrative remarks

In this thesis I highlight the complexity of the spatial relationship of wintering birds with their thermal environment. Species distribution is a multifactorial phenomenon determined by the interaction of multiple thermal and non-thermal environmental variables, whose relative relevance varies according to the ecological context.

Wintering birds respond to natural variations in temperature at multiple scales, from the thermal heterogeneity generated among forest patches by the sun-shade mosaic [Ch. 1] to the large variations in winter temperature registered throughout the Iberian Peninsula [Ch. 7]. However, temperature *per se* accounts for a relatively small proportion of the variation in the distribution of wintering birds, ranging from 5% of foraging patch selection [Ch. 1] to 13% of abundance at landscape scale under harsh weather conditions [Ch. 3], 17-58% of abundance and species richness at regional scale [Ch. 4, 5, 6] and 29% of abundance at peninsular scale [Ch. 7] (partial contributions calculated as $\beta \times r$ in multiple regression models [Ch. 1-6], or as deviance in quantile regression models [Ch7]). Moreover, although woodland species richness was slightly higher in warmer winters [Ch. 4], an extreme cold wave was not sufficient to alter bird abundance and distribution at landscape scale [Ch.3].

Other non-thermal environmental factors seem to be more deterministic in driving winter species distribution than direct measurements of temperature. Among them, the role of vegetation structure stands out, explaining an average of 43% of winter species distribution at landscape and regional scales [Ch. 3, 4, 5, 6]. Similarly, the proximity to potential refuges against predators strongly restricts the subset of forest patches that are suitable to forage (74% of variance, [Ch. 1]). Food availability also influences the abundance and richness of wintering birds, but only for those stable and more predictable resources. While the presence of fruit producing shrubs or the addition of supplementary food in a forest area are important determinants of bird species richness and abundance (36% [Ch. 4] and 48% [Ch. 5], respectively), the biomass of arthropods on the ground, whose availability is subjected to unpredictable snowfalls, exerts no effect on wintering bird populations [Ch. 4].

The thermal state of the environment drives spatial location of species in a complex and multifactorial way, encompassing much more than average temperature. First, species distributions at landscape and regional scales are positively driven by sun radiation, which is modulated by both the topography of the terrain [Ch. 2] and the shade projected by vegetation [Ch. 4]. Sun incidence influences bird distribution at daytime but also at nighttime, when birds select roosting sites anticipating sunshine benefits on foraging conditions the following morning. Altitude exerts a negative influence on bird distributions at regional scales that may also entail notable foresight ability, as birds avoid high altitudes in prevention of future harsh weather episodes [Ch. 4, 5, 6]. Finally, the influence of temperature itself is remarkably different when considering day and night measurements. In a winter scenario where the most limiting period are the long, cold, fasting nights, minimum night temperature is three to five-fold more relevant than daytime temperature determining distribution of birds [Ch. 6, 4].

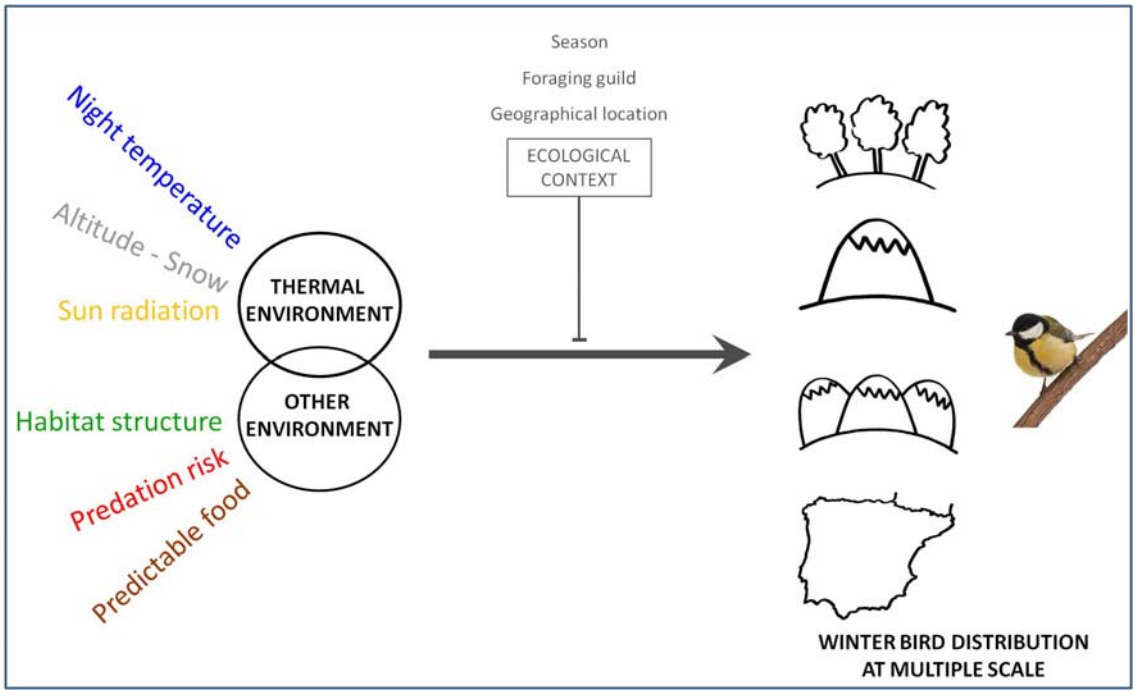
Although this thesis is focused on a very specific system of study (i.e., birds wintering in forests of Guadarrama mountains with continental cold Mediterranean climate; [Ch. 1-6]), some

results are difficult to generalize across species, seasons or geographical locations. For instance, ground-foraging and tree-gleaning birds prioritize different environmental factors for regional distribution [Ch. 4, 5]. Moreover, the same community of forest birds account for a radically different set of environmental factors in winter than in spring, considering the vagabonding life-style to survive in winter and the territoriality inherent to the breeding season [Ch. 6]. Similarly, the effect of sun radiation may only stand out in craggy montane areas with enough topographic heterogeneity affecting sun incidence [Ch. 2].

Applications and prospects

The context-dependence of our results emphasizes the importance of considering the ecological scenario of study, with special attention to the natural history of species. Fine-grained approaches based on the organisms and performed through precise and local measurements of environmental variables are needed to understand the functional mechanisms driving species distribution patterns at broader scales.

The limited and variable effect of temperature on winter species distribution shown from local to peninsular scales highlights the need to control for other environmental factors when predicting the responses of birds to temperature, either under current or future scenarios of global warming. Otherwise, we are at risk of generating strongly biased predictions and of inflating the magnitude of climate change effects, overestimating the influence of temperature on species abundance and underestimating the plasticity of species to respond to temperature changes.



Integración de resultados

En esta tesis se pone de manifiesto la complejidad de las relaciones espaciales entre las aves invernantes y su ambiente térmico. La distribución de especies es un fenómeno multifactorial determinado por la interacción de múltiples variables ambientales térmicas y no térmicas, cuya importancia relativa varía con el contexto ecológico.

Las aves invernantes responden a las variaciones naturales de la temperatura a múltiples escalas, i.e., desde la heterogeneidad térmica que se genera entre parches forestales por el mosaico sol-sombra [Cap. 1] a las grandes variaciones en la temperatura invernal que se registran a lo largo de la Peninsula Ibérica [Cap. 7]. Sin embargo, la temperatura per se explica una proporción relativamente pequeña de la variación en la distribución de las aves invernantes, que oscila entre el 5% en la selección de parches de forrajeo [Cap. 1] hasta el 13% de la abundancia a escala de paisaje bajo condiciones climáticas adversas [Cap. 3], el 17-58% de la abundancia y la riqueza de especies a escala regional [Cap. 4, 5, 6] y el 29% de la abundancia a escala peninsular [Cap. 7] (contribuciones parciales calculadas como $\beta \times r$ en modelos de regresión múltiple [Cap. 1-6], o como devianza en modelos de regresión de quantil [Cap. 7]). Además, aunque la riqueza de especies forestales fue ligeramente mayor en los inviernos más cálidos [Cap. 4], una ola de frio extrema no fue suficiente para alterar la abundancia y la distribución de aves a escala de paisaje [Cap. 3].

Otros factores ambientales no térmicos parecen ser más influyentes en la distribución invernal de aves que la medida directa de la temperatura. Entre ellos destaca el papel de la estructura de la vegetación, que explica una media del 43% de la distribución invernal de especies a escalas paisajísticas y regionales [Cap. 3, 4, 5, 6]. De forma similar, la presencia próxima de refugios potenciales frente a depredadores restringe fuertemente el conjunto de parches forestales adecuados para forrajear (74% de la varianza, [Cap. 1]). La disponibilidad de alimento también influye en la abundancia y riqueza de aves invernantes, pero solo para aquellos recursos más predecibles y estables. Mientras que la presencia de arbustos productores de frutos o la adición de comida suplementaria en un área forestal son determinantes importantes de la riqueza y la abundancia de especies (36% [Cap. 4] y 48% [Cap. 5], respectivamente), la biomasa de artrópodos en el suelo, cuya disponibilidad está sujeta a nevazones impredecibles, no ejerce ningún efecto sobre las poblaciones de aves invernantes [Cap. 4].

El estado térmico del ambiente define la localización espacial de especies de forma compleja y multifactorial, abarcando mucho más que la temperatura promedio. En primer lugar, las distribuciones de especies a escalas de paisaje y regional se ven afectadas positivamente por la radiación solar, que se modula tanto por la topografía del terreno [Cap. 2], como por la sombra proyectada por la vegetación [Cap. 4]. La insolación influye en la distribución de aves durante el día pero también durante la noche, cuando las aves eligen sus dormideros anticipándose a los beneficios de la radiación solar sobre las condiciones de forrajeo a la mañana siguiente. La altitud ejerce una influencia negativa sobre la distribución de aves a escalas regionales que también conlleva una notable capacidad de previsión, ya que las aves evitan las zonas más altas previendo futuros episodios climatológicos adversos [Cap. 4, 5, 6].

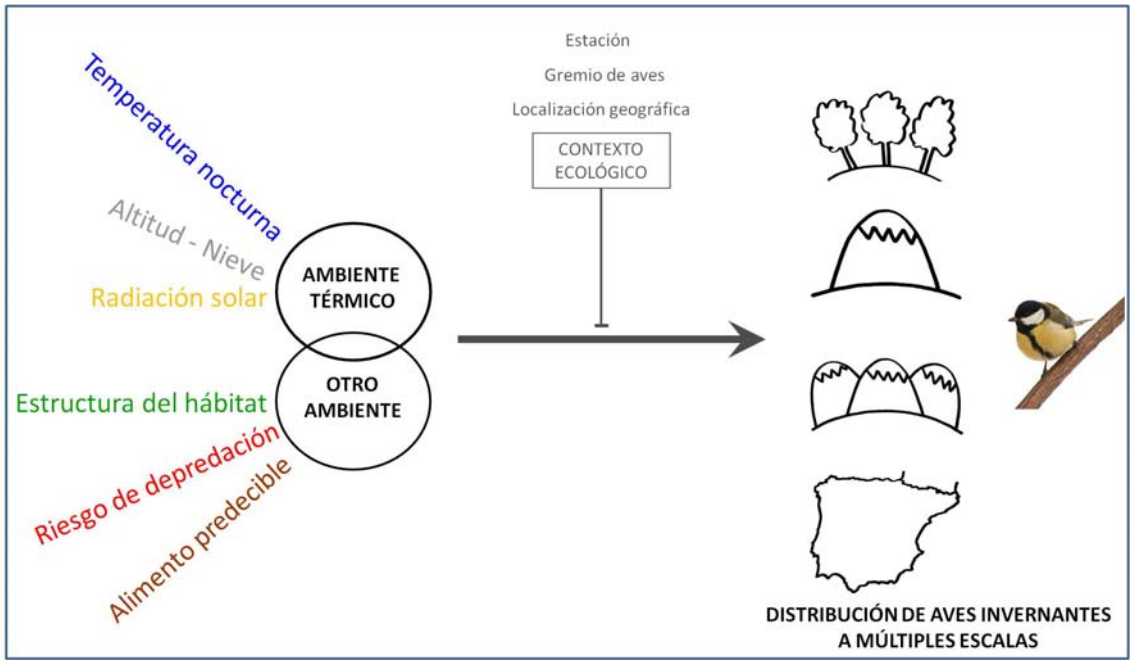
Finalmente, la influencia misma de la temperatura es marcadamente distinta si consideramos las medidas diurnas o nocturnas. En un escenario invernal en el que el periodo más limitante son las largas y frías noches de ayuno, la temperatura mínima nocturna es entre tres y cinco veces más relevante que la temperatura diurna para la distribución de aves [Cap. 6, 4].

A pesar de que esta tesis se centra en un sistema de estudio específico (i.e., aves forestales invernantes en la Sierra de Guadarrama con clima mediterráneo continental frío; [Cap. 1-6]), algunos resultados son difícilmente generalizables a través de especies, estaciones o localizaciones geográficas. Por ejemplo, las aves que forrajean en el suelo y las que lo hacen en los árboles priorizan diferentes factores ambientales en su distribución regional [Cap. 4, 5]. Además, la misma comunidad de aves forestales considera un conjunto radicalmente distinto de factores ambientales en invierno que en primavera, considerando el estilo de vida errante para sobrevivir al invierno y la territorialidad inherente a la estación reproductora [Cap. 6]. De forma similar, el efecto de la radiación solar, debe aparecer solo en áreas montanas escarpadas con suficiente heterogeneidad topográfica que module la incidencia solar [Ch. 2].

Aplicaciones y perspectivas

El carácter contextual de nuestros resultados enfatiza la importancia de considerar el escenario ecológico de estudio, prestando una atención especial a la historia natural de las especies. Las aproximaciones de "grano fino", basadas en los organismos y llevadas a cabo a través de medidas precisas y locales de las variables ambientales, son necesarias para entender los mecanismos funcionales que dirigen los patrones de distribución de especies a escalas mayores.

El efecto limitado y variable de la temperatura sobre la distribución de especies invernantes detectado desde escalas locales a peninsulares resalta la necesidad de controlar otros factores ambientales para predecir la respuesta de las aves a la temperatura, bajo escenarios tanto actuales como de cambio climático. Si no lo hacemos correremos el riesgo de generar predicciones fuertemente sesgadas y de inflar la magnitud del efecto del cambio climático, sobreestimando la influencia de la temperatura sobre la abundancia de especies y subestimando la plasticidad de las especies para responder a los cambios de temperatura.



Conclusions

Conclusiones

Conclusions

- Wintering birds respond to natural variations in temperature at multiple scales. This response varies among local, landscape, regional and peninsular scales.

- The thermal state of the environment drives spatial distribution of birds in a multifactorial way, encompassing much more than average temperature (e.g., nocturnal and diurnal temperatures, sun radiation, altitude).

- Overall, temperature accounts for a relatively small proportion of the variation in the distribution of wintering birds. Other thermal and non-thermal environmental factors seem to be more deterministic (e.g., sun radiation, habitat structure, predation risk, food availability). If these factors are disregarded, we might be inflating the magnitude of global warming effects.

- The relative importance of different environmental factors depends on the ecological scenario under study (e.g., species, seasons, geographical locations). This partially limits our ability of generalization. Organism-based approaches, considering ecological meaningful predictors and developed at fine-grained scales, are needed to understand the functional mechanisms underlying coarser distribution patterns.

Conclusiones

- *Las aves invernantes responden a las variaciones naturales de la temperatura a múltiples escalas. Esta respuesta varía entre escalas locales, de paisaje, regionales y peninsulares.*
- *El estado térmico del ambiente influye en la distribución espacial de las especies de forma multifactorial, englobando mucho más que la temperatura promedio (e.g., temperaturas diurnas y nocturnas, radiación solar, altitud).*
- *En general, la temperatura explica una proporción relativamente pequeña de la variación en la distribución de aves invernantes. Otros factores ambientales tanto térmicos como no térmicos parecen ser más deterministas (e.g., radiación solar, estructura del hábitat, riesgo de depredación, disponibilidad de alimento). Si no tenemos en cuenta estos factores, estaremos inflando la magnitud del efecto del calentamiento global.*
- *La importancia relativa de diferentes factores ambientales depende del escenario ecológico de estudio (e.g., especies, estaciones y localizaciones geográficas). Esto limita parcialmente nuestra capacidad de generalización. Las aproximaciones basadas en el organismo, que consideran predictores con un significado ecológico claro y que se desarrollan a escalas de "grano fino", son necesarias.*

Graphical legend
Leyenda gráfica

Local scale
Escala local

Landscape scale
Escala de paisaje

Regional scale
Escala regional

Peninsular scale
Escala peninsula

High / low nocturnal temperature
Temperatura nocturna alta / baja

High / low diurnal temperatura
Temperatura diurna alta / baja

Temperature effect
Efecto de la temperatura

Sun radiation
Radiación solar

Low altitude
Baja altitud

Supplemented food
Alimento suplementario

Wind speed
Velocidad del viento

Mature / young forests
Arbolado maduro / joven

Vegetation cover
Cobertura de vegetación

Thorny, fruit-producing shrubs
Arbustos espinosos productores de frutos

Roost site
Dormidero

Bird presence
Presencia de aves

Aknowledgements

Agradecimientos

Esta tesis ha sido financiada por una beca de Formación de Personal Investigador (FPI; BES-2009-029386) asociada al proyecto CGL2008-02211/BOS del Ministerio de Economía y Competitividad.

Pienso en estos casi cuatro años de doctorado y me doy cuenta de que he disfrutado mucho, y he aprendido más. Sin duda, en gran parte se lo debo a mis directores: Luisma y Javier.

Mi entera gratitud y admiración a Luisma por su calidad humana y científica, por su gran dedicación y compromiso como director y por su afán de compartir su sabiduría conmigo. Día a día, codo con codo. Todavía me cuesta creer la suerte que he tenido de "caer", casi por casualidad, a su lado.

Mi enorme gratitud también a Javier, por su apoyo inestimable en muchos momentos de este doctorado. Su jovialidad y su cercanía fueron de gran ayuda para encontrar el rumbo en aquellos primeros pasos; e incluso consiguió que se me pegara algo de su amor por los pájaros mientras se nos congelaban los dedos anillando en el Ventorrillo. Siempre han sido fuente de motivación su positivismo, su debilidad por explorar otras posibilidades y por darle "una vuelta de tuerca más" a las cosas.

En muchos momentos he echado de menos una compañera o un compañero en fase pre-doctoral con quien compartir todo lo que para mi era nuevo en este mundo. Sin embargo, con el tiempo he ido apreciando, cada vez más, las ventajas de "nuestro pequeño grupo de investigación". Gracias, Luisma y Javier, por haberme tratado como a una más. Tengo claro que vuestra disposición, la horizontalidad de nuestro grupo y nuestra gran interacción han sido claves en mi motivación.

En segundo lugar debo agradecer la colaboración de los otros co-autores de esta tesis: Óscar y David. A Óscar Gordo por compartir "su" Majada del Cojo en una bonita interacción científica con la que disfruté mucho. A David Palomino por formar parte de la oportunidad que se me brindó de trabajar con los datos del Atlas de las aves en invierno en España 2007-2010; y por extensión a los cientos de participantes del Atlas, que indirectamente son partícipes del capítulo 7 de esta tesis.

A Claire Jasinski por su ayuda desinteresada, leyendo y mejorando el inglés de todos nuestros manuscritos, pero también el de los textos originales de esta tesis. Muchas gracias Claire. A mis padres, por hacer lo propio con los textos en castellano de esta tesis.

A mi familia, por lo mucho que les quiero. Especialmente a mis padres, por dármelo todo y por estar siempre ahí. En este caso, por inculcarme el amor por los estudios desde pequeñita y por enseñarme que podría conseguir lo que me propusiera. Siempre tuve su apoyo para elegir una carrera con un futuro difícil pero maravillosa. Gracias también a mi padre por su infinita e incondicional paciencia para enseñarme matemáticas. A mis abuelos, Carmen y Tomás, por hacerme "una chatilla más de campo que las amapolas"; y a mis abuelos Dolores y Mariano: sí, abuela, al final había tantos pájaros como para estar estudiándolos cuatro años…

A mis pajaritos, a las vacas, los corzos, los zorros y los robles: mi única compañía durante las largas horas de frío en el campo. También a mis esporádicos pero entusiastas acompañantes humanos. A mi madre, por recordarme siempre lo maravilloso que es mi trabajo y por acompañarme cuando no podía más, como durante el temporal frío. A Milli y a Kuku, por brindarme su alegría campestre. A Lusa y Jesús, por animarse a la aventura nocturna de las cajas

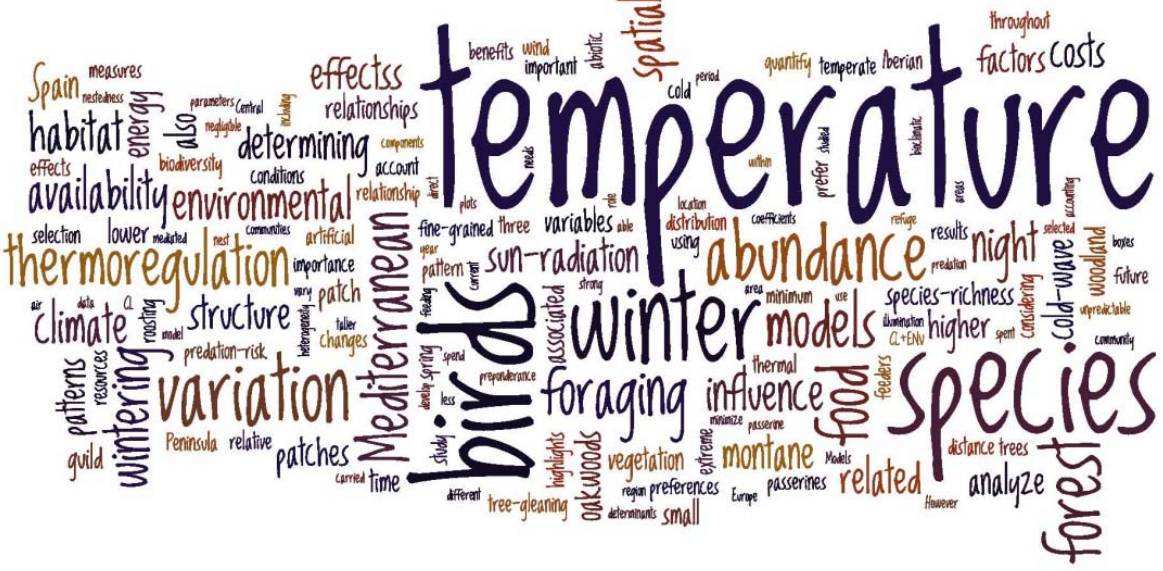
nido. Lusa, nunca olvidaré ese aullido que nos estremeció en medio de la noche (¡!). A Casper y María por esperarme con la estufa encendida en Becerril los días de campo. A Pepe, por su apoyo infinito. A Nino e Inma, por lo significativo de su compañía en la soledad invernal del Ventorrillo.

A mis profesores. Especialmente a aquellos que hace tiempo que se convirtieron en un referente, a los que recuerdo con un profundo cariño. Gracias a Begoña Fernández y a Pedro del Castillo, de la UAM. También a Pilar Cubas y Mar Trillo del CNB, por iniciarme con mimo en esto de la investigación.

A Edu, por ser el mejor compañero y amigo que podría haber imaginado. Te he echado de menos en el doctorado. A Anita, mi compañera del doctorado por excelencia, de vidas paralelas que por fin se unieron, bien fuerte. Gracias por los momentos acequia, también a Ana y a Celia. Y por abrirme la puerta de esa pequeña gran familia que es el grupo de F. Valladares y que me ha alegrado el último año de tesis. Muy feliz de haberos conocido y muy agradecida por esta adopción inesperada. Gracias: Elena, Xandra, Jorge, Tere, Inés, Cris, Dulce, Ali, Jorge, Ana, Fernando, Ana y Joao.

A mis compañeros del labo de F. Bozinovic de la PUC en Santiago de Chile, por acogerme con los brazos abiertos en mi primera estancia en Chile. Gracias Pancho y Cote por practicar la mezcla perfecta entre pega y hueveo. Gracias Dani por llevarme a los cerros, me encantó conocerte. Gracias Sabri, Tami, Naty, Nuria, Vane, Andrés… por hacerme sentir en la cato como en casa. Santiago sigue en mi corazón, también sus gentes, Casa Italia y Néstor.

A los habitantes de Puerto Williams, por una de las experiencias más especiales de mi vida. A J. Jiménez por su profesionalidad y a R. Reyes por su apoyo desinteresado, tanto logístico como científico. A Ronnie, Tami, Bryan, Cristian, Gonzi y Kitty como núcleo de una familia muy especial. Bryan, PW sin ti no habría sido lo mismo, ya lo sabes. A Miguel, Gina, Gini y Tania por ser unas personas tan maravillosas. A Patty por su simpatía, a Jaime Ojeda por su buena onda y a Nico por su ayuda en terreno. A Julia, los amigos de Villa Ukika, de la Alianza Roja, del Árbol y del baby-fut Navarino por dar color al invierno. A la señora Catalina y a Gonzi por los matesitos y la buena conversa junto a la vodka los días de terreno en Bahía Guanaco. A leñadores, vaqueros, marinos, pacos, ambulancia, personal del aeropuerto y a todos aquellos que me ahorraron largas caminatas en terreno alguna vez. Pucha que Chile me prendió…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The ecological consequences of global warming are of general concern in a changing world, and predictions of species distributions have mainly focused on temperature. Nevertheless, species may respond to much more than temperature.Here I investigate whether temperature is as important driving current species distributions as usually assumed, and compare its relevance with that of other environmental factors, with special attention to the thermal environment.These queries are tackled on birds wintering in the Iberian Peninsula, in a multi-scale approach from forest patches to landscape, regional and peninsular scales.Fine approaches at lower scales are the base to understand the functional mechanisms underlying distribution patterns at coarser scales